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SIDA CONTRIBUTIONS TO BOTANY

VOLUME 12 NUMBER 1 MAY 1987

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SIDA Contributions to Botany

25 years

of

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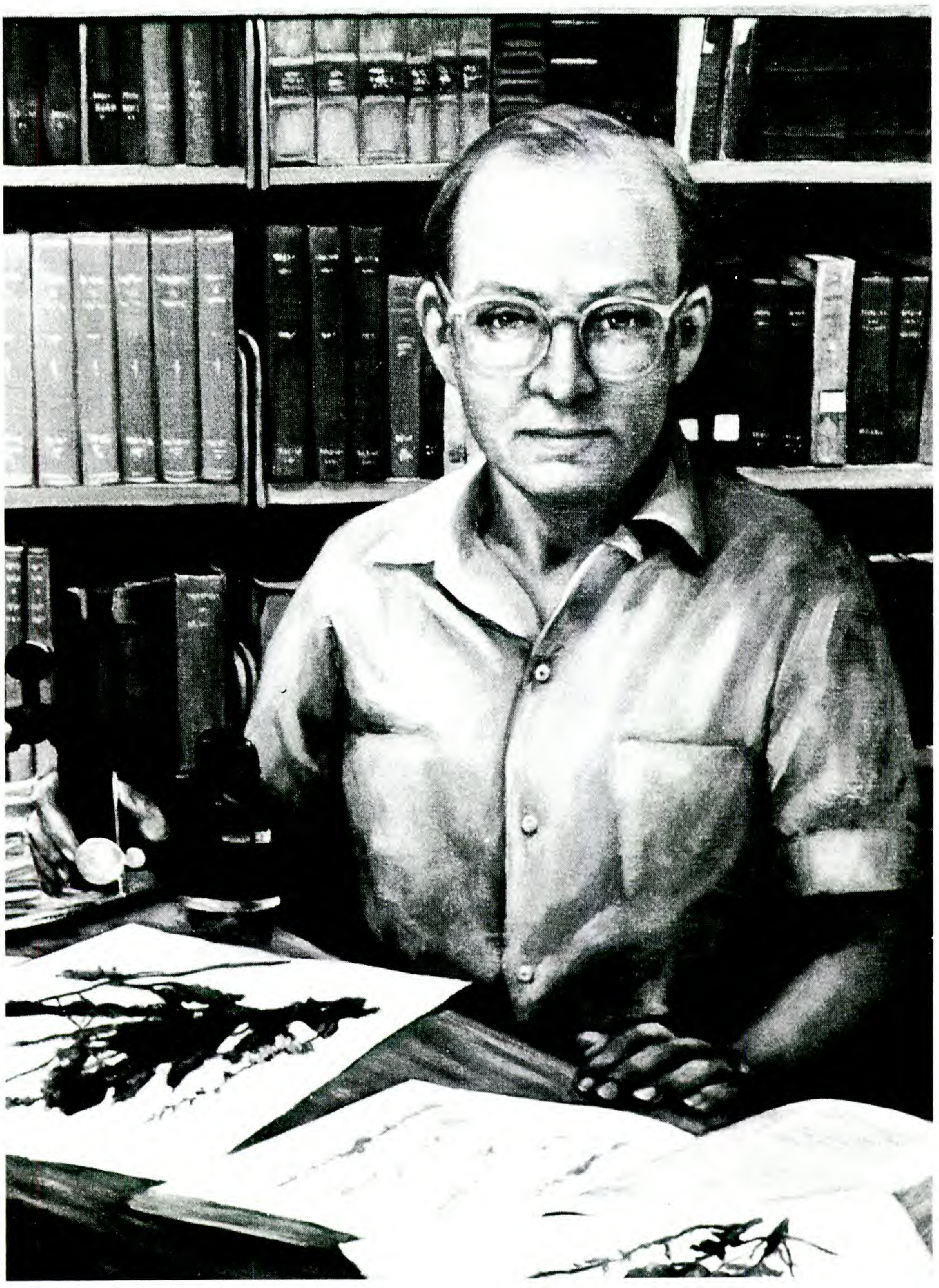
"Blessed are the

floristic workers . . ."

— Lloyd H. Shinners

SIDA 12(1): 1 – 3. 1987.



LLOYD HERBERT SHINNERS
22 Sep 1918—16 Feb 1971

This portrait, by Betty Sampson, is
located in the Science/Engineering Library.

25th ANNIVERSARY

This year marks the 25th anniversary of "Sida, Contributions to Botany." Dr. Lloyd H. Shinners founded the journal in 1962 and chose the name "Sida" because it was short and easy to cite in the literature and it was a generic epithet of a genus that was cosmopolitan and recognizable by botanists around the world.

Upon Dr. Shinners death in 1971, the subscriptions had reached about 340 and today, 16 years later, the subscriptions are over 600. Of this number, over one-third are foreign, one-third are U.S. institutions and ca one-third U.S. individuals.

This issue is dedicated to the subscribers, researchers, and reviewers that make this scientific journal what it is today. Thanks to all of you.

Wm. F. Mahler, Publisher
Barney L. Lipscomb, Editor
John W. Thieret, Associate Editor

THE SMU HERBARIUM[1]

BARRY M. COHEN

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DR. SHINNERS' IVY TOWER IN THE BASEMENT

Tucked away in the depths of the Science and Engineering Library at Southern Methodist University (SMU) in Dallas, Texas, is found the SMU Herbarium, formally known as "The Lloyd H. Shinners Collections in Systematic Botany" (1). From its variant names, we see that we are actually discussing two distinct collections.

First we have the collections of plants itself which justifies the term herbarium. This collection of plants gathered from around the world is complemented by an excellent library on plant taxonomy. In order for such a collection to be of the maximum research value to the botanical scientist, any plant collection must be supported by the appropriate literature germane to the actual plants collected. The fundamental purpose of any herbarium is to enable the botanist to make specific identification of individual plants and to allot them to their proper classification. These necessary standards are more than admirably met by the SMU Herbarium; and additional research studies in geology, anthropology, and medicinal uses of plants may be undertaken there.

Although founded in 1940 by Dr. Cyrus Longworth Lundell, an eminent explorer and plant collector, the SMU Herbarium most emphatically bears the stamp of the genius and character of Dr. Lloyd H. Shinners. In 1948 when Dr. Lundell's interests directed his energies toward agriculture and the development of the Texas Research Foundation at Renner, Texas, his associate, Dr. Shinners, a Canadian who had come to the herbarium in 1944 armed with a doctorate in botany from the University of Wisconsin, was ready to assume the position of acting director. In 1949 he was appointed director and promoted to full professor of botany at SMU in 1960 (2).

Today in the United States, the SMU Herbarium ranks 24th in the number of plant specimens and somewhere between 12th and 15th in its library collection. The number of plants held by the herbarium is now well

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[1]A graduate paper prepared in partial fulfillment of the course requirements for SLIS 5290 *Special Collections and Archives, North Texas State University, School of Library and Information Sciences, Denton, Texas, 17 December 1986.*

SIDA 12(1): 4—9. 1987.

over 382,00 while the library holdings are on the order of 10,000 volumes with many unusual and rare items in each collection (3).

The plant collection has been assembled by a variety of methods customarily employed by all herbariums. First there have been the acquisitions made by the staff's work in the field collecting plants from all over the world, but the concentration has been on the plants indigenous to the Southwest. Dr. Shinners own contributions are noteworthy. His extensive and rapid collecting expeditions earned him the sobriquet, first in derision, but then of respect, "The Postcard Botanist." Dr. Shinners appeared to be everywhere, and wherever he was, he worked with rare dedication. For several summers during the early 1950's, rather than taking his vacation, Dr. Shinners worked gratis at the Missouri Botanical Garden in St. Louis, asking only for payment in duplicate specimens for the SMU collection (4).

Some other individuals' principal contributions to the herbarium have also been in field work. For example, V.L. Cory, after retiring in 1945 as a range botanist for the State of Texas, collected thousands of specimens every year for the SMU Herbarium until 1952 when he "retired" for the second time (5). Dr. Eula Whitehouse, a herbarium staff member and researcher until her own retirement in 1958, made one foreign trip and a world collecting expedition. In 1952 Dr. Shinners reported, in February and March, 1952, she made a brief excursion to East Africa, going by air via London (with brief visits to Kew Gardens and bookstores), Rome, Cairo, and Khartoum (6). Two years later in 1954 – 1955 she undertook her world expedition:

> Dr. Whitehouse was away from September to January on a round-the-world trip to collect and to visit botanists and botanical gardens, covering 37,000 miles, with stops in Cyprus, Syria, India, Thailand, Malaya, Java, Australia, New Zealand, Fiji, and Hawaii. The kindness of many botanists en route in undertaking to dry and ship her specimens greatly facilitated her travels. Packages are still arriving, and exchanges of specimens and publications are still being arranged (7).

Dr. Whitehouse possessed an avid interest in the cryptograms (ferns and mosses) and consequently, SMU has a noticeably strong collection in this area.

Other developments for the herbarium have been in the area of identification and exchange. The herbarium exchanges duplicate specimens with many other institutions. In addition, when individual collectors request an identification, it is the custom to "pay" for the service by giving the herbarium making the identification one specimen of the plant in question.

There is also a practical side to identification. From time to time the

herbarium is called upon by hospitals to identify plants which have been ingested by someone, often children, causing an adverse reaction. The police will rush the offending plant to the curator, for identification, and he then consults with the physician. Treatment, if needed, can be given the patient quickly.

In conjunction with its exchange and identification program, SMU has an active loan program to and from related herbarium institutions. This program is directed by the curator, Mr. Barney Lipscomb. The plants after being pressed, dried, and mounted are wrapped in blank newsprint by bundles of twenty-five, and shipped Library Rate by the United States Post Office. Thus last year the SMU Herbarium provided some 2,500 specimens for outside research, while bringing in some 2,900 items for faculty and other researchers at SMU. When specimens are returned to their home herbarium (usually after six months), they are accompanied by a set of annotations made by the botanical scholars. With these annotations, the specimens become even more valuable for future use. Lipscomb uses the micro-computer to keep track of the loan program. His data file includes the books and serials on interlibrary loan. Extremely valuable materials, mostly the rare books, or plants with limited specimens, are not sent on loan (8).

Gifts have been an important source in building both the plant and library collections. One plant collection is particularly noteworthy. In 1959 Dr. Shinners reported an impressive gift consisting of the private herbarium of Dr. Delzie Demaree. Known to his colleagues as either "Old Scratch" or "Arkansas Demaree," this Indiana born (1889) scholar with his botany Ph.D. from Stanford (1932), was also known as having one of America's outstanding private plant collections. Having taught in every type of educational situation from elementary school to Tulane University, and having lived and collected in every part of the country from the Hopi Indian Reservation to Florida, Dr. Demaree had built an especially strong herbarium from the plants of Arkansas, Louisiana, and East Texas. Aged sixty at the time of his "bequest," Dr. Demaree is still living at an active age of ninety-seven. Over the years he has given SMU thousands of plants and continues even after the death of his friend Dr. Shinners in 1971 to include SMU as a depository of his now local expeditions (9). As Dr. Shinners noted in 1959, the Demaree Herbarium is "one of the largest single gifts of the kind ever made to an American institution, ranking with the presentation of Asa Gray's herbarium to Harvard" (10).

Gifts were also the foundation for the SMU Herbarium Library. Many of these works were donated or inherited from the private libraries of either Dr. Shinners or Dr. Whitehouse.

The library received as a gift from Dr. Shinners the 1769 volume of Plukenet's *Opera*, in four quarto volumes, a highly important early reference in connection with the identification and early geographic distribution of plants. This ranks with Morison's *Historia Plantarum* (1680) and Dillenius's *Hortus Elthamensis* (1732), each in two folio volumes, which we already had, and marks the culmination of 15 years of searching (11).

Other rarities include the complete works of DeCandolle. Also there is an unusual set of the works of Linnaeus (in Dutch, 1761). We find first editions of Charles Lyell's three-volume *Principles of Geology* (1830 – 1833) and one of Gilbert White's *Naturalist's Calendar* (1795), as well as a valuable illustrated second edition of White's more famous *Natural History of Selbourne* (1834).

The present library has some interesting reference works. Dr. Shinners was especially proud of a plant literature catalogue, rare in the 1950's and now printed by the publisher G.K. Hall in its final closed form, *The Index to American Botanical Literature*: 1886 – 1966. The herbarium has kept as a reference tool its old Card Catalogue to Plant Literature from the Gray Herbarium Library at Harvard, even while subscribing to the modern microfiche version in order to remain current. Even in microfiche, SMU is only one of some twenty libraries to have access to the Gray Catalogue. Moreover, the SMU Herbarium is one of only half-a-dozen libraries to own a microfilm set of the *Index to Specimens Filed in the New York Botanical Garden's Vascular Plant Type Herbarium*. This work, published in 1985, costs $7500.

Access to the botanical literature in the herbarium collection itself is facilitated by the Shinners' Revised Dewey Decimal System for Geographic Botany (Floras, etc.). This unique system of classification consists of rigorous divisions of material either by plant *genus* or by geographic designation. Both are more detailed than the standard Dewey. Although some herbariums have discussed adoption of the Shinners' Dewey, to date none has made the modifications required. Most herbariums still employ the Dewey System, but a few have adopted the Library of Congress Classification.

The library also houses the archives of Dr. Shinners which were donated by his sister upon his death in 1971. These are composed of a card catalogue, two file cabinets full of material arranged by subject (mostly uncompleted projects), and four large boxes of correspondence in no particular order. The correspondence is in good condition, but some care should be taken to transfer the material to acid-free Hollinger boxes and to remove the dangerous yellowing letters (mostly foreign correspondence) before they cause any further damage. This author, following standard archive procedure, has suggested that the letters should be put in chronological

order with some record of the person or institution addressed by Dr. Shinners and the return correspondence. Lipscomb, however, is of the opinion that the material would be of more use to the herbarium if it were indexed by the type of plant discussed in each letter. In the future, perhaps both projects can be undertaken.

In 1971 another SMU professor of botany, Dr. William F. Mahler, became director of the herbarium. He continues another of Dr. Shinners' traditions, namely the publication of the journal *Sida, Contributions to Botany* (*Sida* is a genus of plants) founded in 1962. Both Dr. Shinners and more recently Dr. Mahler are of the opinion that research can be encouraged by a scholarly forum. From a librarian's point of view *Sida* is of interest. It was originally a highly irregular serial that has become regular with two issues per year. *Sida* appeared with six issues per volume over a two year period, but in 1970 there is a seventh issue of vol. 3 in a third year. And part of vol. 4 was published and appeared before the end of vol. 3 (12). Dr. Mahler stabilized the publication issuing two numbers per year with four numbers constituting a volume. There are plans for a *Herbarium Quarto* as a newsletter and for a *Sida, Botanical Miscellany* to appear also on an irregular basis. *Sida* is highly regarded in the world of botany and is exchanged for journals that would otherwise not be available to SMU.

Lipscomb, as herbarium curator, has by custom become the botanical bibliographer for the SMU Science-Engineering Library. He selects the works to be ordered. Once the volumes arrive, he assigns them a Shinners' Dewey Number and turns them over to Mrs. Sandra Setnick. Although a reference librarian, Mrs. Setnick supervises the book-ordering and cataloging through the central library system at SMU. When the books return from the cataloging department, they are usually placed in the herbarium library in the basement.

Conrad Gesner (1516 – 1565) is known in the library world as the "founder of bibliography." Botanists have, on the other hand regarded him as "the leading modern scholar up to the time of Linnaeus." (13). The psychological combination of these two fields is understandable since classification is so important to both disciplines. The Renaissance genius of Gesner was reflected by Dr. Shinners and his colleagues, past and present. That is the historical heritage of which the SMU Herbarium and the herbariums around the world are a part.

ACKNOWLEDGMENTS

Much of the paper concerning the SMU Herbarium is based on observation as well as information provided by Mr. Barney Lipscomb to the author during the fall of 1986. The author is grateful to Mr. Lipscomb for his

help, and for making available the reports upon which this study is based. Thanks are also in order for Mrs. Sandra Setnick and Dr. William F. Mahler who aided the research greatly. Where no citations appear in the text, it may be assumed that the information is based upon personal interviews. My thanks also to Dr. Doralyn Hickey, of the School of Library Science at North Texas State University, Denton, Texas.

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THE SHINNERS' REVISED DEWEY DECIMAL[1]

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The primary purpose of the Southern Methodist University Herbarium is the taxonomy of plants, especially those of the southwestern United States. Dr. Lloyd H. Shinners, an early and long-time director of the herbarium not only was engaged in his professional duties of plant classification, but also took a keen interest in bibliographic classification. This concern led to the development of a unique bibliographic classification system for use in the SMU Herbarium Library, now known as "The Shinners' Revised Dewey Decimal for Geographic Botany" (Floras, etc.). This particular classification scheme was formulated by Dr. Shinners in response to special needs arising from both the herbarium's physical location within the SMU Science-Engineering Library and its working agreement with the cataloging department of the SMU Central University Library.

In 1961 the herbarium moved from its old headquarters in the attic of the Fondren Science Building to the basement of the Science-Engineering Library. It was apparently decided, by simple mutual understanding, that the herbarium's library would be cataloged in the main and science-engineering catalogs, but no separate card catalog would be maintained for the herbarium itself. Dr. Shinners hence needed and wanted some method of classification for his own library, and one that would work in conjunction with that of the science-engineering catalog. From these conditions grew the Shinners' Revised Dewey.

The Shinners' system as presently constructed is, by this writer's observation, apparently based on Dewey's tenth edition, for no Dewey edition before or since has had the Shinners' feature of relating a specific number to a given plant taxon. In 1963 Shinners mentions in an internal memorandum that he is in the process of converting from Harvard's Gray Herbarium classification to the Dewey, but does not specify the edition (2). For his system Dr. Shinners made use of the botanical class numbers 580 – 589. With these he incorporated the numerical system developed by Dr. C.G. De Dalla Torre and H. Harms in their book *Genera Siphonogamarum* for the Spermatophyta or seed plants.

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[1]A term paper in partial fulfillment of the course requirements for SLIS 5220.

SIDA 12(1): 10 – 12. 1987.

The *Genera Siphonogamarum*, published in Leipzig in 1907, is a monumental work written except for the bibliographic references, entirely in Latin. Professors Dalla Torre and Harms designated 280 families of Spermatophyta by numerical assignment, sometimes with a letter added to the number where there are closely related families or where there is some controversy concerning the designation itself. Beside each plant family name is a set of numbers which refer to the numbers assigned to the genera within each family. Within the text each family or genus is followed by its original bibliographic citation. In the literature of taxonomy the first reference with a definitive description is the most important concerning that individual taxon, for it is usually the one on which the botanical name is based. Other literature is, of course, important, but the most relevant is the initial article or description.

The incorporation of this system by Dr. Shinners is ingenious, for it provides not only a numerical designation for a large group of plants, but also a ready-made if now somewhat dated bibliography. (See item #3)

The Shinners' Revised Dewey utilizes the Dewey geographic tables to classify floras of various regions, states, and countries. Since becoming director in the early 1970's, Dr. William Mahler has updated the classification system to include the Pteridophyta, Bryophyta, and Lichenes. The SMU Herbarium possesses an unusually fine collection of ferns, mosses, and lichens and consequently desired to bring the library collection concerning these plants within the overall classification scheme.

How does the Shinners' Revised Dewey work? Let us report some examples as demonstrated by Barney Lipscomb, the curator of the herbarium. For the title *The grasses of Bahia* (in Brazil), the first decision must be whether to employ a specific plant designation or choose a geographic one. If approached from its "flora" aspect, 581.981 for Spermatophytes in Brazil could be used. However, this is much too broad a classification and the better choice would be 584 for Spermatophyta monographs plus .019 for grasses or the Gramineae (Poaceae); hence in this case the book would carry the call number 584.019. Another example demonstrated was *Forest Trees of Australia*. The choice made here was to classify immediately by flora since the geographic feature of this work is so prominent. The designation would then be 581.994 for a geographic study of the Spermatophyta in Australia. Once Lipscomb assigns the Shinners' Revised Dewey number, the library materials are processed by the central cataloging department, given their Cutter numbers, and a card prepared for them with "Herbarium" written above the full call-number. The cards are then filed both in the main catalog at Fondren and in the catalog of the Science-Engineering Library.

By custom Lipscomb has become the library's bibliographer for botanical works. In addition to the works installed in the herbarium, there are more general ones which must be placed in the main collection, either reference or circulating. These books are given Library of Congress numbers. The herbarium collection contains the only newly assigned Dewey numbers in the SMU science-engineering area. However, there are some older botanical works with Dewey numbers that have not been converted to the Shinners' System.

The results of this system are what Dr. Shinners intended for himself and the herbarium library staff. Any work can easily be located given either a title or geographic area plus the author's name, without climbing the stairs and consulting the card catalog. Lipscomb's ability to locate titles is truly remarkable. However, it does require more than casual practice with the Shinners' Revised Dewey. However, sometimes the research and thought needed in the most difficult of searches, e.g. by name of author only, is more time consuming than the tedious walk up the stairs, but rather easily conventional search of the card catalog.

The Shinners' Revised Dewey was developed to meet the particular needs of the SMU Herbarium. From time to time, other herbaria express interest in the system, but none has adopted it as yet.

The Shinners' Revised Dewey also has some logical connection with what the Library of Congress Classification does when it gives a geographic specification by "Cuttering according to Region or Country" (1). However, the exact application by the Library of Congress varies throughout the classification scheme and the individual libraries have great leeway in assigning the proper Cuttering for their collections. In any event, the SMU Herbarium finds its unique classification system worthwhile in its own circumstances, and it seems to serve its purpose well.

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SIDUS SIDARUM VI.—THE *SIDA MARTIANA* (MALVACEAE) COMPLEX IN MÉXICO

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in cooperation with
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In my recent treatment of the North and Central American species of *Sida* (Fryxell 1985), I included *S. xavieri* Monteiro as occurring in México. It has been pointed out to me (Krapovickas, pers. comm.) that *S. xavieri* is best treated as a synonym of *S. martiana* St.-Hilaire, a view with which I am in agreement.

It further came to my attention that the Mexican plants that I included under *S. xavieri* (= *S. martiana*) in fact represent several distinct species. It is my purpose here to distinguish and characterize these species.

This species complex can be referred to *Sida* sect. *Nelavagae* Borssum Waalkes on the basis of its 5-carpelled fruits, its characteristic calyx morphology and pigmentation, and its leaf form (cf. Fryxell 1985, p.68). Within the section this complex allies itself with those species that have glabrous (or nearly glabrous), muticous fruits and often have setose stems and petioles and glandular pubescence. The species may be distinguished according to the following key.

a. Flowers subsessile, aggregated into dense axillary glomerules or in axillary pedunculate "heads" ..... *S. urens* L.
a. Flowers manifestly pedicellate, usually solitary in the axils or aggregated into more or less open paniculate inflorescences.
  b. Upper leaf surface with appressed simple (non-glandular) hairs 0.5 – 1 mm long; staminal column pubescent or glabrous; pedicel shorter than the subtending leaf.
    c. Corolla yellow or salmon, sometimes drying violet; staminal column pubescent; petioles 1/3 – 1/2 length of blades; calyx 5 – 7 mm long ..... *S. monticola* Fryx.
    c. Corolla pale yellow; staminal column glabrous; petioles ca 1/4 length of blades; calyx 7 – 8 mm long ..... *S. michoacana* Fryx.
  b. Upper leaf surface with minute glandular or stellate hairs; staminal column glabrous; pedicel subequal to subtending leaf.
    d. Calyx 4 – 5(– 7) mm long, the midrib of each lobe dark-pigmented (Fig. 4); upper leaf surface stellate-pubescent, without purplish blotch along midvein ..... *S. alamosana* S. Wats.
    d. Calyx 6 – 9 mm long, the midrib of each lobe not dark-pigmented; upper leaf surface with minute, simple (glandular) hairs, sometimes with purplish blotch along midvein.

SIDA 13(1): 12 – 21. 1987.

e. Pedicels 1.5 – 5 cm long; petals 8 – 9 mm long . . . . . *S. anodifolia* Fryx.
e. Pedicels 0.5 – 2 cm long; petals 5 – 6 mm long . . . . *S. martiana* St.-Hilaire

Sida martiana St.-Hilaire was described on the basis of Brazilian material (Type: Villa do Principe, Minas Geraes, *St.-Hilaire s.n.*, P as photo F-35573), as was *Sida xavieri* Monteiro (Type: Brazil, Paraibo, João Pressoa, *Xavier 342*, RBR?). *Sida martiana* occurs beyond Brazil as far as Venezuela (*Fryxell & Burandt 4339*) and Panamá (*Nee 10132* and *10164*) but is not known farther north. The other species discussed here occur in México, *S. urens* L. being of wide distribution and also found in Central and South America and Africa. The new species are described below.

Sida **anodifolia** Fryxell, sp. nov. (Fig. 1)

Frutices erecti caulibus dense viscidis setosisque; laminis foliorum late ovatis cordatis, grosse crenatis vel serratis, supra pilis simplicibus adpressis 0.2 – 0.5 mm longis et saepe macula irregulari purpurea secus nervum centralem; pedicellis usque 5 cm longis folium subtentum subaequantibus; calycibus 7 – 8 mm longis viscidis flavo-virentibus sed marginibus atrovirentibus; petalis flavidis, 8 – 9 mm longis; fructibus glabris, mericarpiis 5 muticis.

Erect shrub to 1.5 m tall or ascending subshrub, the stems densely covered with minute glandular hairs and with scattered simple hairs 2 – 3 mm long. Leaf blades ovate, simple (or with very weak tendency for lobing), basally cordate, coarsely crenate or dentate, acute or acuminate, usually 2 – 3 cm long (1.25 – 1.82 times as long as broad), palmately 5-nerved, the upper surface with appressed simple hairs 0.2 – 0.5 mm long, the upper surface sometimes with an irregular purple blotch along the midvein (as in some species of *Anoda*), the lower surface with minute stellate hairs and some simple hairs (especially on veins); petioles half the length of the blade to longer than blade, with pubescence like stem; stipules < 1 mm long. Pedicels solitary in the leaf axils, slender, 1.5 – 2 cm long in flower to 3 – 5 cm long in fruit, often equaling the subtending leaf, glandular-pubescent, articulated 5 – 9 mm below the flower; calyx 7 – 8 mm long, evenly covered with minute glandular hairs, ca half-divided, the lobes trullate, obscurely veined, yellowish-green with dark-green margins (the midribs not dark); petals yellow, 8 – 9 mm long, minutely and inconspicuously pubescent in the sinuses of the claws, otherwise glabrous; staminal column glabrous, pallid, ca 3 mm long; filaments 20 – 30, 2 – 3 mm long, the anthers yellow, the pollen orange-yellow; styles 5, slender, glabrous, pallid, the stigmas capitellate, purplish. Fruits oblate, ca 5.5 mm diameter, glabrous, blackish at maturity; mericarps 5, muticous, 1-seeded.

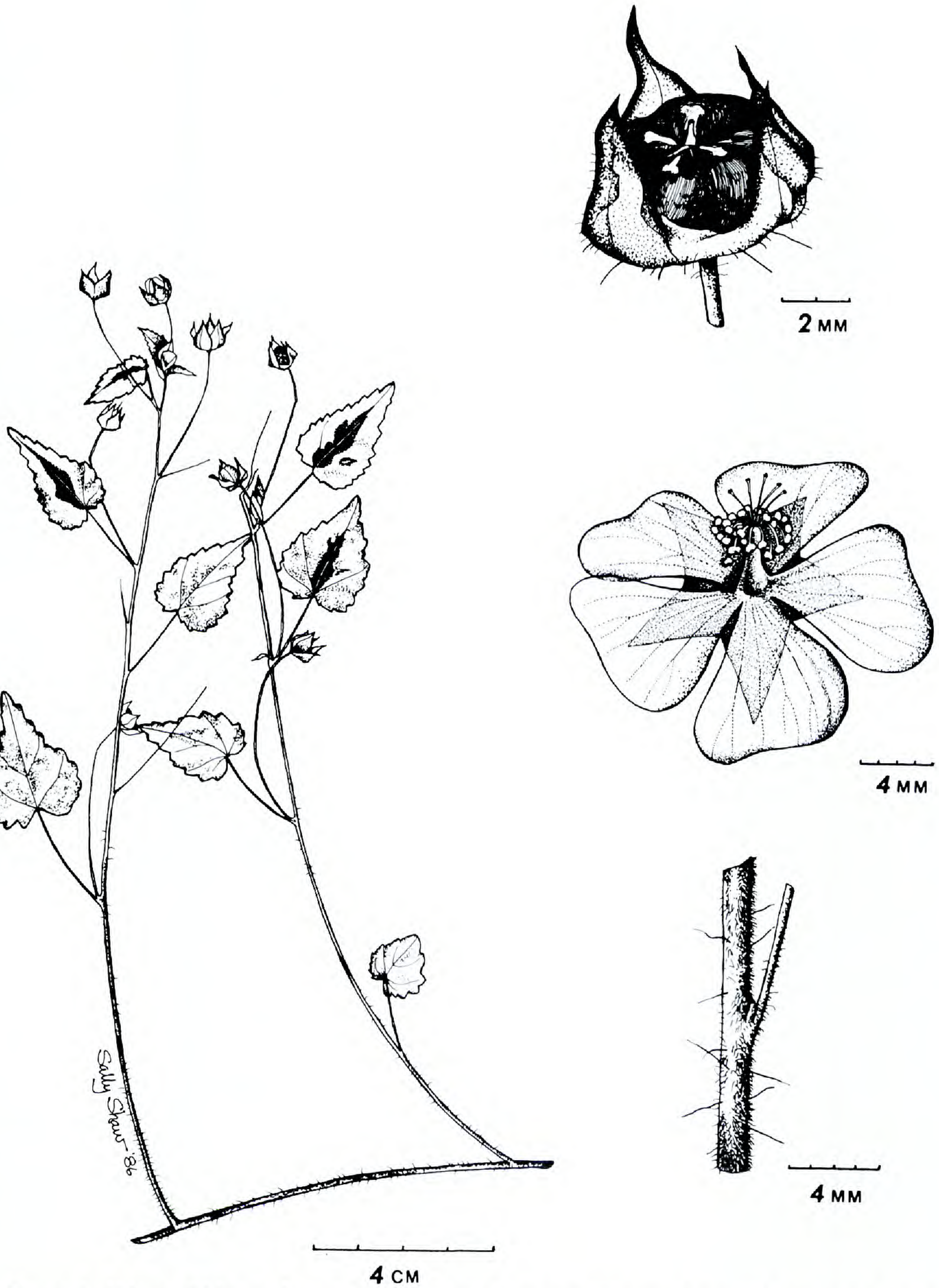

Figure 1. *Sida anodifolia*. a, flowering and fruiting branch; b, fruit; c, flower; d, portion of stem showing pubescence (*Koch et al. 79470*).

TYPE: MÉXICO: OAXACA, Mpio. de Pluma Hidalgo, terracería a Tultepec, 1 km al E de la carretera Pochutla-Oaxaca 16 km al N de Pochutla; sabana con encinos y *Curatella*; alt. 320 m, común, flores abriendose después de medio dia, 12 Nov 1979, *Koch, Fryxell, & Wendt 79502* (HOLOTYPE: CHAPA; ISOTYPES: BH, BM, BR, CAS, CTES, ENCB, MEXU, NY, pf).

PARATYPE: OAXACA, Mpio. de San Pedro Mixtepec, terracería a San Gabriel Mixtepec, 3.2 km al N de San Pedro Mixtepec, 24 km al N de Puerto Escondido, bosque caducifolio con elementos de bosque semicaducifolio, alt. 325 m, frecuente en vegetación densa en sitios perturbados, 10 Nov 1979, *Koch, Fryxell & Wendt 79470* (CAS, CHAPA, CTES, ENCB, F, K, MEXU, MICH, XAL, pf).

The specific epithet is chosen in reference to the purple blotches on the leaves that resemble those that are characteristic of certain species of *Anoda* (and of the related *Periptera*). The intensity of expression of these blotches is variable (being strongly expressed in no. *79502*, weakly so in no. *79470*); it is presumably related to the degree of exposure (or shading) of the individual plant and the amount of insolation impinging on it. Similar blotches occur (also variably) in *Sida martiana*, but this phenotype is otherwise unknown to me in *Sida* and is thus sufficiently distinctive to merit the choice of epithet. The leaf outlines labelled "S. xavieri" in Fryxell (1985, fig. 2, I–J) represent *S. anodifolia*.

SIDA **michoacana** Fryxell, sp. nov. (Fig. 2).

Herba ascendens caulibus dense viscidis setosisque; foliis anguste ovatis acuminatisque, supra pilis adpressis simplicibus 0.5 – 1 mm longis, petiolis quam laminis ca 1/4-plo longioribus; calycibus 7 – 8 mm longis, dense viscidis setosisque, marginibus et venis loborum atroviridis; petalis 6 – 8 mm longis luteolis; fructibus 3 – 3.5 mm diametro glabris, mericarpiis 5, muticis, parietibus lateralibus chartaceis.

Ascending herb reclining on and supported by other plants, the young stems green, densely glandular-pubescent and with scattered to dense simple (non-glandular) hairs 1 – 2 mm long. Leaf blades ovate-cordate, crenate, acuminate, up to 12 cm long, at least twice as long as wide, gradually smaller and narrower toward apex, the upper surface with scattered simple or bifurcate appressed hairs 0.5 – 1 mm long, the lower surface with 2 – 4-armed stellate hairs (simple hairs on veins); petioles viscid and setose like stem, up to 3.5 cm long (ca 1/4 length of blade); stipules subulate, 2 – 3 mm long, glabrous or ciliate. Inflorescence diffusely paniculate; pedicels slender, 10 – 23 mm long, densely viscid, articulate 3 – 4 mm below the flower; calyx 7 – 8 mm long, densely viscid and setose, ca half-divided, the lobes trullate, pale yellow-green with dark green margins and veins; petals pale yellow, 6 – 8 mm long, densely pubescent on margins of claw, otherwise glabrous, subequal to calyx; staminal column pallid, glabrous, 2 mm long, the filaments ca 2 mm long, the pollen orange; styles 5, slender, pallid, the stigmas truncate, pallid,

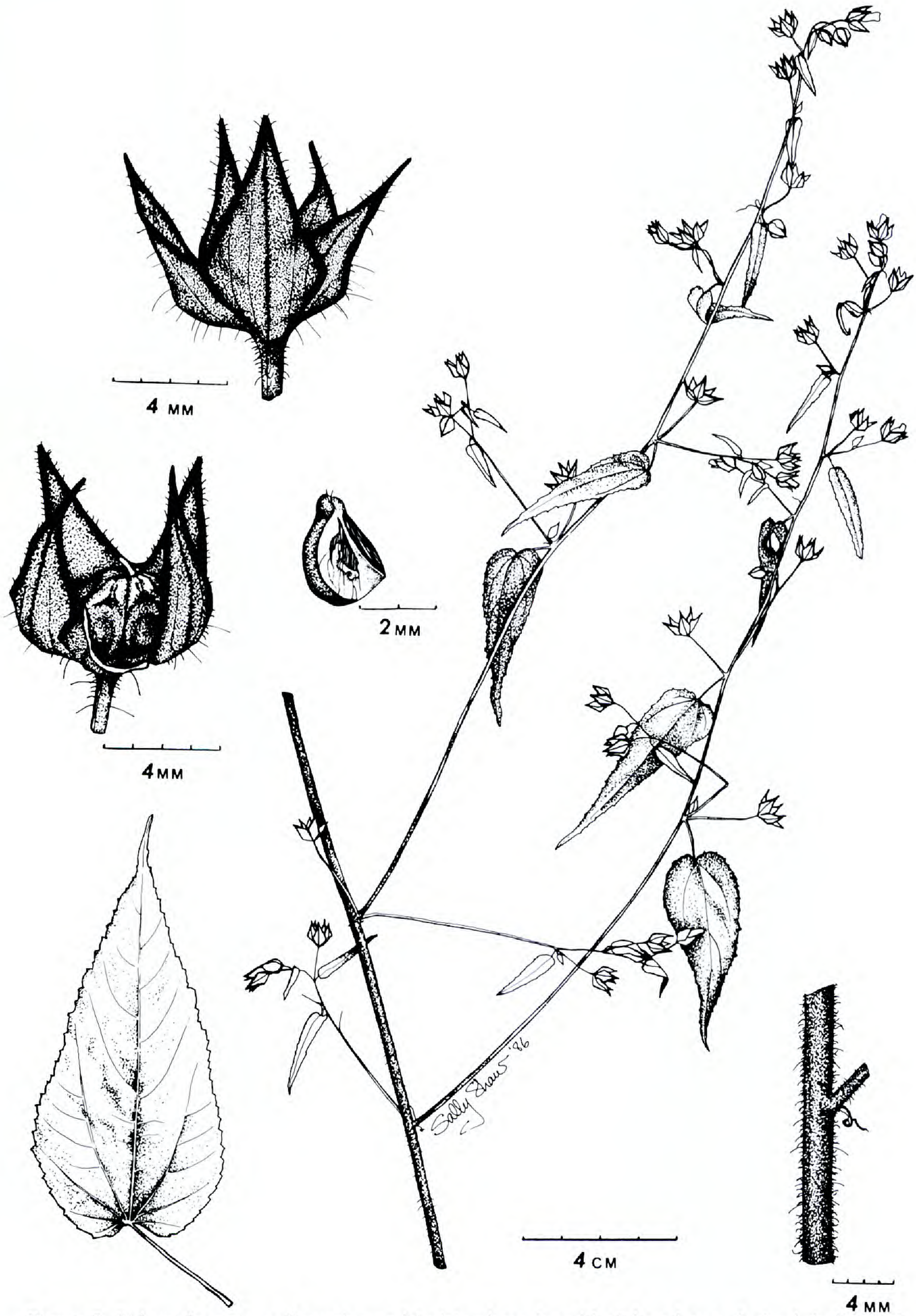

Figure 2. *Sida michoacana*. a, flowering and fruiting branch and leaf; b, calyx; c, fruit; d, individual mericarp, showing fragile lateral wall; e, portion of stem showing pubescence (*Koch & Fryxell* 8353).

slightly exceeding the androecium. Fruits enclosed in calyx, oblate, 3 – 3.5 mm in diameter, glabrous; mericarps 5, muticous, 2.5 mm long, the lateral walls fragile, chartaceous; seeds solitary.

TYPE: MÉXICO: MICHOACÁN, Mpio. Benito Juárez, 43 km al S de Zitácuaro, por la carr. a Huetamo, bosque espinoso de *Acacia* y *Mimosa* con claros con pastizal; suelo arcilloso; alt. 910 m; hierba acostándose sobre otras plants, tallos víscidos, flores amarillo-anaranjado pálidas; en el lecho de un arroyo, escasa, 8 Nov 1983, *Koch & Fryxell 8353* (HOLOTYPE: CHAPA; ISOTYPES: BM, CTES, MEXU, MICH, pf).

PARATYPE: MÉXICO: Edo. México, Distr. Temascaltepec, Cumbre de Tejupilco, 2000 m, oak woods, 24 Nov 1932, *Hinton 2708* (NY).

Superficially, *Sida michoacana* resembles *S. glabra* Miller, but may be distinguished from it most readily by the larger calyces, the glabrous muticous mericarps, and the simple appressed hairs on the upper leaf surface. The fragile, chartaceous lateral walls of the mature mericarp are distinctive. The specific epithet is in reference to its geographical distribution.

SIDA **monticola** Fryxell, sp. nov. (Fig. 3).

Suffrutices caulibus viscidis setosisque; lamina foliorum anguste ovatis, irregulariter serratis, supra pilis simplicibus adpressis 0.5 – 1 mm longis; pedicellis usque 1.5 cm longis quam folium subtentum brevioribus; calycibus 5 – 7 mm longis dense pubescentibus pilis glandularibus atque stellatis, viridis pallidis marginibus atroviridis; petalis 7 – 8 mm longis in sicco violascentibus; fructibus glabris mericarpiis 5 muticis.

Subshrub 1 m tall, the older stems purplish, covered with long simple hairs (1 – 1.5 mm long), a few stellate hairs, and innumerable small glandular hairs. Leaf blades ovate, cordate, up to 5.5 cm long, 3.5 cm wide, (1.4 –) 2 – 3 times as long as broad (smaller and narrower upward), irregularly crenate-serrate, acute or acuminate, discolorous, the upper surface with appressed simple (occasionally stellate) hairs 0.5 – 1 mm long, the lower surface with erect stellate hairs (simple hairs on the veins); petioles up to 2.5 cm long (1/3 – 1/2 length of blade) with pubescence similar to that of stem; stipules subulate, 1 – 2.5 mm long, somewhat recurved, 1-nerved. Flowers solitary in the leaf axils but tending to form terminal panicles; pedicels slender, 8 – 15 mm long (generally shorter than the subtending leaf), articulated 3 – 4.5 mm below the flower, with both glandular and long simple hairs; calyx 5 – 7 mm long, densely covered with glandular and stellate hairs, ca half-divided, the lobes trullate, the margins dark-pigmented; petals "salmon" sometimes drying violet, 7 – 8 mm long, minutely pubescent on margins of claw, otherwise glabrous; staminal column 1.5 – 2 mm long, pallid, pubescent, the filaments apical, 1 – 1.5 mm long, the anthers and pollen yellow or orange; styles 5, slender, glabrous, pallid, the stigmas capitate, pallid, exceeding the

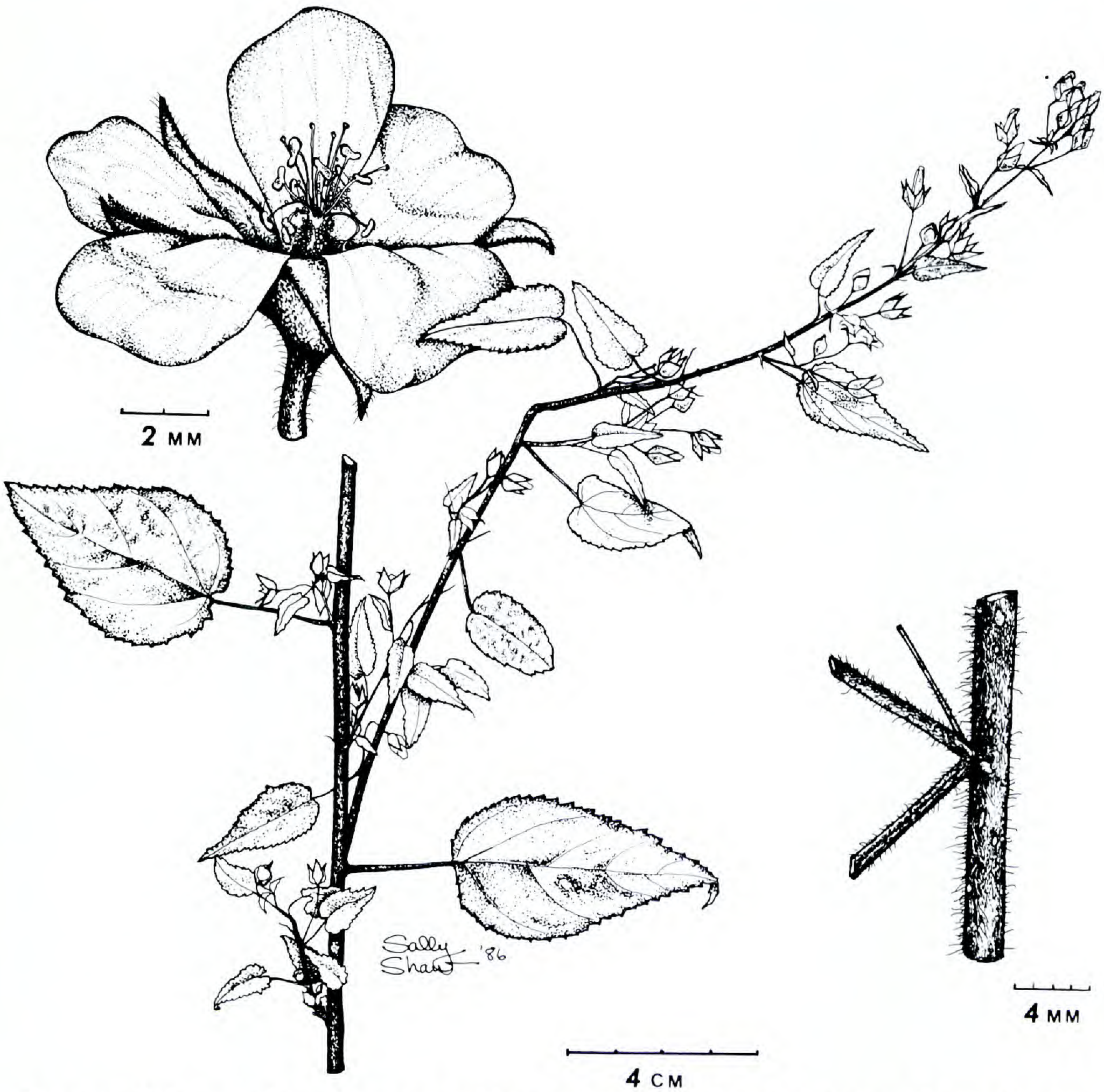

Figure 3. *Sida monticola*. a, flowering and fruiting branch; b, flower; c, portion of stem showing pubescence (*Koch & Fryxell 83272*).

androecium. Fruits ca 4 mm diameter, glabrous (or apically pubescent); mericarps 5, muticous, essentially indehiscent and unornamented, 1-seeded.

TYPE: MÉXICO: GUERRERO, Mpio. de Chilpancingo, camino a El Tejocote, 9 km al oeste del entronque con carretera Chilpancingo-Acapulco (17 km al S de Chilpancingo); alt. 1970 m, 25 Nov 1983, *Koch & Fryxell 83272* (HOLOTYPE: CHAPA; ISOTYPES: CTES, MEXU, pf).

PARATYPE: MÉXICO: OAXACA, Monte Albán near Oaxaca, Oct 1894, *Smith 643* (NY).

Sida monticola ("mountain dweller") is so named to call attention to the relatively high elevation at which it grows. Its distinguishing features are indicated in the key.

The Mexican species distinguished here exhibit essentially discrete

Figure 4. *Sida alamosana*. a, flowering and fruiting branch; b, calyx (*Sanders et al. 4263*).

geographic distributions. *Sida alamosana* (Fig. 4) is the most northerly, growing in the states of Sonora, Chihuahua, and Sinaloa in the Sierra Madre Occidental and adjacent coastal regions at elevations of 0 – 1000 m. *Sida michoacana* grows in the states of Michoacán and México at elevations of 1000 – 2000 m in the Transverse Volcanic Belt. *Sida monticola* is found in Guerrero and Oaxaca at elevations of 1000 – 2000 m in the Sierra Madre del Sur. *Sida anodifolia* occurs in Oaxaca along the Pacific Coast at about 300 m elevation. By contrast, *S. urens* has a relatively wide distribution, being found from Nayarit to the Yucatán peninsula, generally at low elevations, and also in other tropical counties beyond México.

ACKNOWLEDGMENTS

I am grateful to Sally Shaw for the illustrations and to Antonio Krapovickas for shared ideas about *Sida*, and to S.D. Koch and T.L. Wendt for collaboration in the collection of some of the specimens cited herein.

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SIDUS SIDARUM VII.—THE GENUS *SIDA* (MALVACEAE) IN AUSTRALIA

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A perusal of Australian floras (e.g., Bentham 1863; Bailey 1899–1905; Ewart & Davies 1917; Gardner 1930; Black 1943–1957) reveals a number of species assigned to the genus *Sida*. Recent studies (Fryxell 1978, 1985) have clarified the limits of this genus and of segregate and related genera, as a result of which it is possible to conclude that only eight Australian species are assignable to *Sida* proper, and the remaining species are assignable to other genera. Most of these remaining species pertain to the genus *Sidastrum* (cf. Fryxell 1978), but a few (e.g. *S. inclusa*, *S. platycalyx*) seem to fit neither in *Sida* nor in *Sidastrum*, so that another disposition may prove necessary. The purpose of the present paper is to deal with the eight species that pertain to *Sida* proper. A consideration of those species deserving transfer to *Sidastrum* is beyond the scope of this paper.

The eight species include three species (four taxa) that are endemic to Australia and five species that occur in other parts of the world as well. Four of these five are more or less pantropical or even cosmopolitan; the fifth (*S. parvifolia*) has a more limited distribution (certain shores of the Pacific and Indian Oceans) and is here reported for the first time from northern Australia.

The eight Australian species are distinguished in the following key, after which the species are discussed individually. According to the sectional analysis of the genus presented earlier (Fryxell 1985), the Australian species may be allocated as follows:

Section *Sidae*—*S. rhombifolia*, *S. acuta*
Section *Spinosae*—*S. spinosa*, *S. parvifolia*
Section *Cordifoliae*—*S. cordifolia*, *S. rohlenae*, *S. atherophora*, *S. magnifica*

KEY TO THE AUSTRALIAN SPECIES OF SIDA SENS. STR.

a. Carpels 5.
  b. Plants small, more or less prostrate and spreading; leaves no more than 2 cm long ..... 5. *S. parvifolia* DC.
  b. Plants erect, often 1 m tall or more; leaves usually more than 2 cm long ..... 8. *S. spinosa* L.

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a. Carpels 6 – 14.
  c. Mericarps muticous.
    d. Petals 10 – 20 mm long; calyx to 10 mm long . . . . . 4. *S. magnifica* Domin
    d. Petals 6 – 9 mm long; calyx 8 – 8.5 mm long . . . . . .
    . . . . . 7a. *S. rohlenae* var. *mutica* (Bentham) Fryxell
  c. Mericarps each with two apical spines.
    e. Spines of mericarps retrosely barbed.
      f. Leaves narrowly oblong; flowers solitary, axillary; mericarps 6 – 10.
        g. Herbage puberulent (hairs 0.2 mm or less), the stems (usually) also with long (1 mm) simple hairs; leaves coarsely serrate . . . . . 7. *S. rohlenae* Domin var. *rohlenae*
        g. Herbage densely stellate-pubescent (hairs 0.5 mm or more); leaves finely denticulate . . . . . 2. *S. atherophora* Domin
      f. Leaves cordate-ovate; flowers crowded; mericarps 10 – 12 . . . . . 3. *S. cordifolia* L.
    e. Spines of mericarps glabrous or pubescent, if pubescent the hairs not retrorsely oriented.
      h. Leaves distichous, concolorous; pedicels less than 1 cm long, subequal to petioles; mericarps 8 – 10 . . . . . 1. *S. acuta* Burm. f.
      h. Leaves spirally disposed, discolorous; pedicels 1 – 3 cm long, exceeding the petioles; mericarps 10 – 14 . . . . . 6. *S. rhombifolia* L.

1. Sida acuta Burman f., Fl. Indica 147. 1768. Lectotype: JAVA, *s. coll., s.n.* (G).

Numerous synonyms are cited by Borssum Waalkes (1966) and by Fryxell (1985), many from tropical Asia. The species is pantropical and is often a prominent component of the weed flora.

2. Sida atherophora Domin, Biblioth. Bot. 22:945. 1928. Type: QUEENSLAND, auf den Sandstein Hügeln der Dividing Range bei Jericho verbreitet, *Domin 6542* (lectotype: PR-529144!).

Sida atherophora var. *brachypoda* Domin, Biblioth. Bot. 22:945. 1928. Type: QUEENSLAND, Sandstein Hügeln der Dividing Range bei Jericho, *Domin 6546* (holotype: PR!).

Sida atherophora is distinguished from *Sida rohlenae* var. *rohlenae* primarily by differing pubescence and leaf form. The two Australian endemics appear to be closely allied. *Sida atherophora* appears to be significantly less common than *S. rohlenae*, apparently confined to central Queensland (Fig. 1).

Representative specimens: QUEENSLAND: Mitchell District, ca 6 mi E of Jericho, *Smith & Everist 992* (BRI, CANB); Leichhardt District, area surrounding State Wheat Board installations on sandy soil, *Henderson 229* (BRI, CANB).

3. Sida cordifolia L. Sp. Pl. 684. 1753. Type: "cordifolia 4" (holotype: LINN-866.12!).

Sida densiflora Domin, Biblioth. Bot. 22:946. 1928. TYPE: QUEENSLAND, grasige Stelle im Emu Park bei Rockhampton, auf Sandboden, *Domin 6505* (HOLOTYPE: PR!)

Numerous other synonyms are given in Borssum Waalkes (1966) and Fryxell (1985). *Sida cordifolia* is pantropical and subtropical in distribution.

4. SIDA MAGNIFICA Domin, Biblioth. Bot. 22:946. 1928. TYPE: NORD-QUEENSLAND, grasige und steinige Hügel am Walsh River nördlich von Chillagoe, *Domin 6548* (HOLOTYPE: PR-529152!).

Sida dallachyi C.T. White, Proc. Roy. Soc. Queensl. 47:54. 1936. TYPE: N. QUEENSLAND, Mt. Molloy, *Brass 2449* (HOLOTYPE: BRI!).

Sida magnifica is evidently restricted to northern Queensland. It is distinguished by relatively large flowers and foliage and by muticous mericarps, a character that it shares with *S. rohlenae* var. *mutica*.

5. SIDA PARVIFOLIA DC. Prodr. 1:461. 1824. TYPE: Réunion (Bourbon), *Bory s.n.* (HOLOTYPE: G-DC, as microfiche!).

Sida discolora E.G. Baker, J. Bot. 30:291. 1892 (non Hooker f., 1834). TYPE: "Timor" [Sumba], *Teysmann 10809* (HOLOTYPE: K). See Borssum Waalkes (1966, p. 193) concerning the type locality.

Although Borssum Waalkes (1966) describes this as "a rare species," I suspect on the basis of our field observations in northern Australia that this is not so much a rare species as it is an inconspicuous species that is on that account seldom collected. Moreover, it appears to be confined to coastal sands, so that only botanists working on the seashore have a chance of encountering it. Borssum Waalkes states that "in Malesia it prefers coralline sea shore sites and a seasonally dry climate," which is in conformity with our observations. Its distribution extends to the Philippines and islands of the Indian and Pacific Oceans.

The discovery of *Sida parvifolia* constitutes a new record for Australia, and the specific collections are as follows (cf. Fig. 1):

NORTHERN TERRITORY: 3 km NE of Point Blaze [12°55′S, 130°10′E]; monsoon forest along beach; scarce in beach sand, 22 Jun 1985, *Fryxell & Stewart 4877* (CANB, pf). **Cobourg Peninsula**, Port Essington on eastern shore at Turtle Point [11°13′S, 132°05′E]; perennial herb from woody rootstock; common in sand just above high tide line, 25 Jun 1985, *Fryxell, Craven & Stewart 4922* (CANB, pf); Table Head on E shore of Port Essington [11°14′S, 132°10′E]; perennial herb, abundant on sand back of beach, 26 Jun 1985, *Fryxell, Craven & Stewart 4927* (CANB, pf). **Arnhem Land**, on shore of Arafura Sea, ca 6 km N of mouth of King River at Turner Point [11°47′S, 133°31′E]; prostrate perennial herb, common on front line of beach dune, 26 Jun 1985, *Fryxell, Craven & Stewart 4937* (CANB, pf).

6. SIDA RHOMBIFOLIA L. Sp. Pl. 684. 1753. TYPE: "2 rhombifolia" (HOLOTYPE: LINN-866.3!).

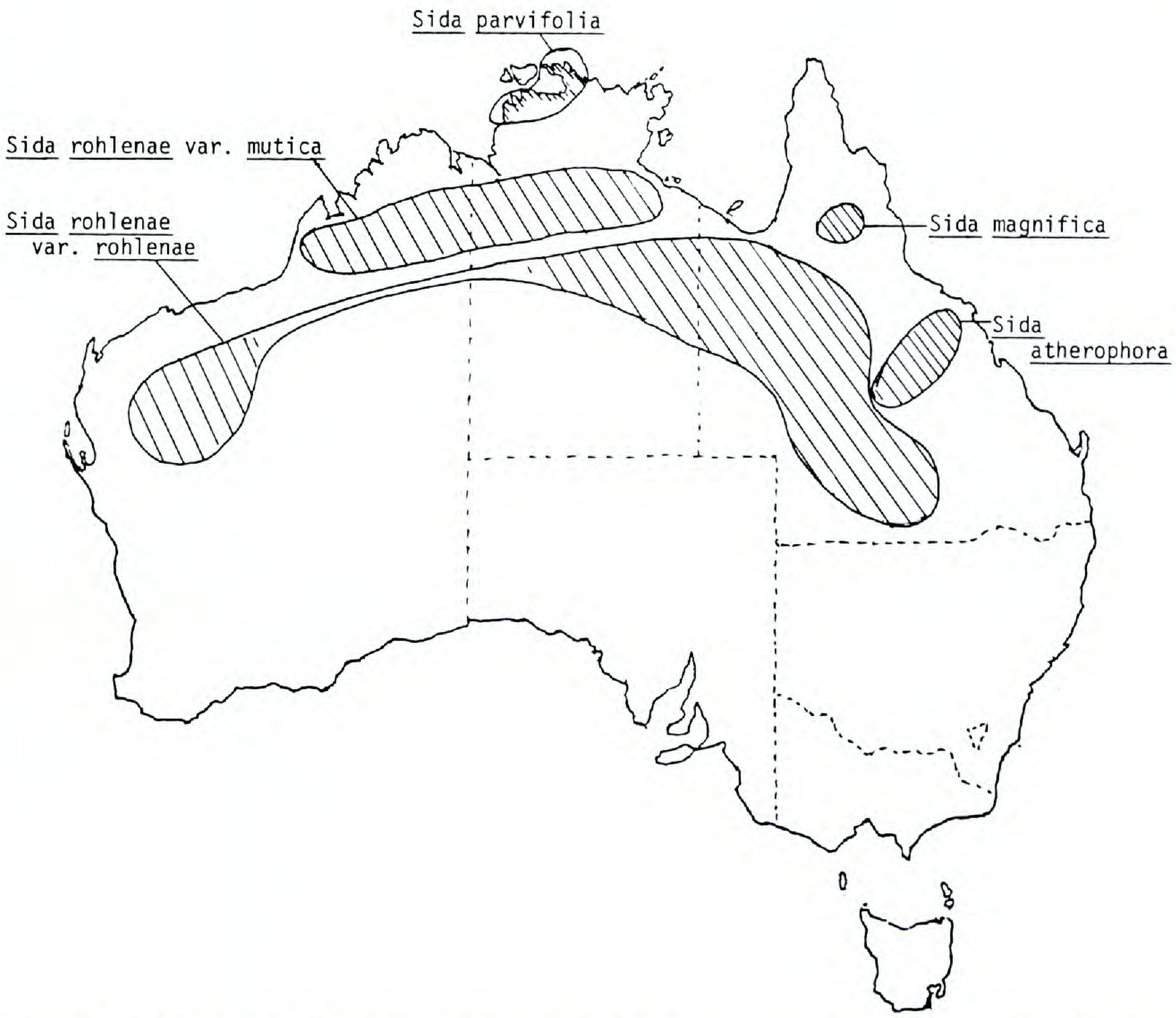

Figure 1. Approximate distribution of species of *Sida* (sens. str.) endemic to Australia, plus *S. parvifolia*, newly reported for Australia.

Numerous synonyms are cited by Borssum Waalkes (1966) and Fryxell (1985), none based on Australian plants. This species is pantropical and subtropical in distribution and reaches temperate climates to a limited extent as an annual. Several authors have subdivided it into varieties and subspecies, but these distinctions are not relevant to its occurrence in Australia.

7. SIDA ROHLENAE Domin var. ROHLENAE, Biblioth. Bot. 22:944. 1928. TYPE: QUEENSLAND, grasige Hügel bei Cloncurry, *Domin* 6538 (HOLOTYPE: PR!).

Sida rhombifolia L. var. *incana* Bentham, Fl. Austral. 1:196. 1863. SYNTYPES: Nicholson River, *Mueller s.n.*: Comet River, *Leichhardt s.n.*

Representative specimens:

WESTERN AUSTRALIA: Kennedy Range, E of Mooka Homestead, *Wilson* 8458 (PERTH, pf).

NORTHERN TERRITORY: Old MacDonald Downs Homestead [22°27′S, 135°14′E], *Latz* 5776 (NT, pf); Gibsons Ck., 35 mi N of Tennant Creek [19°10′S,

134°10′E], *Must 197* (CANB, DNA, NT, pf); Huckitta Out-station, 14 mi dam [22°44′S, 135°01′E], *Dunlop 2052* (MEL, NT, pf); 10 mi S of Banka Banka [18°57′S, 134°00′E], *Dunlop 2044* (CANB, DNA, NT, pf); 81 km S of Dunmarra on Stuart Hwy., *Fryxell, Craven & Stewart 4442* (CANB, pf).

QUEENSLAND: Maranoa Distr., Noondoo, near Dirranbandi, *Everist 792* (BRI, pf).

7a. Sida rohlenae var. **mutica** (Bentham) Fryxell, comb. nov. Basionym: *Sida cordifolia* var. *mutica* Bentham, Fl. Austral. 1:197. 1863. Type: McArthur River, Gulf of Carpentaria, 1837, *Mueller s.n.* (K!). *Sida mutica* (Bentham) Domin, Biblioth. Bot. 22:945. 1928 (non Delile ex DC., 1824).

The present variety is distinguished from *Sida rohlenae* principally by the muticous mericarps, which in var. *rohlenae* have two prominent apical spines that are retrorsely barbed. There seem to be no intergrades. The two taxa appear to be otherwise indistinguishable, and so they are recognized in varietal rather than specific rank. Variety *mutica* is distributed relatively to the north of var. *rohlenae* (Fig. 1).

Representative specimens:

WESTERN AUSTRALIA: road to Beagle Bay, N of Broome, *Fryxell, Craven & Stewart 4551* (CANB, pf), *Fryxell 3859* (pf), *Maconochie 1178* (CANB, NT); Mt. Anderson Station, Fitzroy Valley, *Royce 6921* (PERTH, pf); Kimberley Downs Station, *Fryxell & Craven 3935* (CANB, pf); 30 km N of Gibb River Homestead, *Fryxell & Craven 3979* (CANB, pf).

NORTHERN TERRITORY: Keep River, *Pullen 10891* (CANB); ca 2 mi S of Larrimah, *Fryxell, Craven & Stewart 4428* (CANB, pf); McArthur River, 2 km S of Caranbirini waterhole [16°17′S, 136°04′E], *Rice 2267* (CANB).

8. Sida spinosa L. Sp. Pl. 683. 1753. Type: "spinosa" (holotype: LINN-866.1!).

Numerous synonyms are cited in Fryxell (1985), mostly based on plants from tropical America. The species is widespread, often weedy, in tropical, subtropical, and temperate regions in both hemispheres.

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I am grateful to the curators of the several herbaria cited herein, who have made available specimens on loan or who have provided welcome and assistance during visits to the collections under their care. I am also grateful to L. A. Craven and J. McD. Stewart for companionable collaboration in collecting some of the specimens cited above.

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NEW SPECIES OF *PHAEDRANASSA* AND *EUCHARIS* (AMARYLLIDACEAE)[1]

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ABSTRACT

Phaedranassa brevifolia is described from Ecuador. Chromosome number of *P. brevifolia* is $2n = 46$, as has been reported for other species of the genus. *Eucharis moorei*, *E. cyaneosperma*, and *E. formosa* are described from Ecuador and Amazonian Peru and Colombia. *Eucharis moorei* is putatively the most primitive species in the genus, with many ancestral characters of the genus. All three *Eucharis* species have a chromosome number of $2n = 46$, the most common somatic number in the genus. Karyotypic differences between Peruvian and Ecuadorean *E. formosa* are reported.

Monographic and floristic work on Andean Amaryllidaceae of "infrafamily" Pancratioidinae (sensu Traub 1957, 1963) has necessitated recognition of the following new species in *Phaedranassa* Herbert and *Eucharis* Planchon & Linden.

MATERIALS AND METHODS

Root tips for karyotype analysis were pretreated for 2 hours at room temperature in a 10 ppm solution of o-isopropyl-N-phenylcarbamate (Storey and Mann 1967), fixed in a 3:1 mixture of 95% EtOH at 18° C for 24 hours, and subsequently stored in 70% EtOH at 18° C. Root tips were hydrolized in 1N HCL at 50° C for 2 − 3 minutes, squashed, and stained with iron aceto-carmine. As absolute chromosome length can vary appreciably from cell to cell due to differential affects of pre-treatment (Tjio and Hagberg 1951; Schlarbaum and Tscuchiya 1984), relative length, based on a value of 100 for the haploid complement, was used to designate size class. Relative size classes are based on 80% or better correlations between absolute size class (modified from Battaglia, 1955) and relative length (RL) of mitotic metaphase preparations of various species of *Eucharis*, *Eucrosia*, *Phaedranassa*, and other Amaryllidaceae with $2n = 46$, all of which have similar relative length ranges. RL $\geq$ 7.0 [absolute length (AL): $>$ 10 μm] = large, 5.0 − 7.0 (AL: 7 − 10 μm) = moderately large, 3.5 − 5.0 (AL: 5 − 7 μm) = medium, $\leq$ 3.5 (AL: 2 − 5 μm) = small. Chromosome

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morphology, modified from Battaglia (1955), is defined as follows: metacentric, Arm Ratio (AR; long arm/short arm) = 1.00 − 1.10; nearmetacentric, AR = 1.10 − 1.50; submetacentric, AR = 1.50 − 3.00; subtelocentric, AR = > 3.00.

Leaf samples were fixed in FAA, treated for, and examined with scanning electron microscopy as reported for fresh pollen in Meerow and Dehgan (1985).

A NEW SPECIES OF PHAEDRANASSA

Phaedranassa is a small, primarily Ecuadorean genus closely allied to *Eucrosia* Ker-Gawler, *Rauhia* Traub, and, more distantly, to *Stenomesson* Herbert (Meerow 1987). Species delimitation within *Phaedranassa* is frequently cryptic, and almost completely obscured in herbarium specimens. Foliage characters often provide important indicators for species delimitation, yet leaves of most species are hysteranthous, and therefore usually absent from dried collections. I have collected the genus widely in Ecuador in 1982 and again in 1984, and have also received living material from various colleagues. Comparative study of this material suggests that the following collection represents an undescribed species.

PHAEDRANASSA **brevifolia** Meerow, sp. nov. (Figure 1).

A *P. cinerea* Ravenna et *P. tunguraguae* Ravenna foliis minoribus et insigniter amphistomaticis, floribus paucioribus et brevioribus, perianthii tubo concolori, tepalis luteo-vittatis, et filamentis et stylo roseis differt.

Glabrous bulbous geophyte. Bulb sub-globose with a dark brown tunic, 3.5 − 4.5 × 4.5 − 5.5 cm; apical neck short, 13 − 20 mm long, 10 − 12 mm diam. Leaves 2, mostly hysteranthous, 1 sometimes present at anthesis, petiolate, non-glaucous; petiole sub-terete, 8.5 − 12 cm long, ca 3 − 4 mm thick; lamina narrowly elliptic, 13 − 16 cm long, 3 − 5 cm wide, apically short acuminate, basally attenuate to the petiole, dark green adaxially, whitish-green abaxially and densely striate (Figure 2), the striae more or less parallel, amphistomatic. Inflorescence umbellate, terminated by 2 lanceolate bracts which enclose the flowers before anthesis; scape terete, 39 − 56 cm tall, ca 6 mm diam. proximally, 2.2 − 3 mm distally, solid proximally, with a narrow diameter hollow cylinder in the distal half; bracts 23 − 28 mm long, ca 7 mm wide; inner bracteoles successively narrower and thinner. Flowers 5 − 7, funnelform to ventricose, declinate to sub-pendulous, pedicellate; pedicels 15 − 17 mm long; perianth 3.5 − 4 cm long, consisting of 6 tepals in two whorls basally connate into a short tube; tube sub-cylindrical, ca 7 mm long, pink, constricted at its juncture with the ovary, 2.8 mm at the base, 4.5 − 5.2 mm wide at the throat,

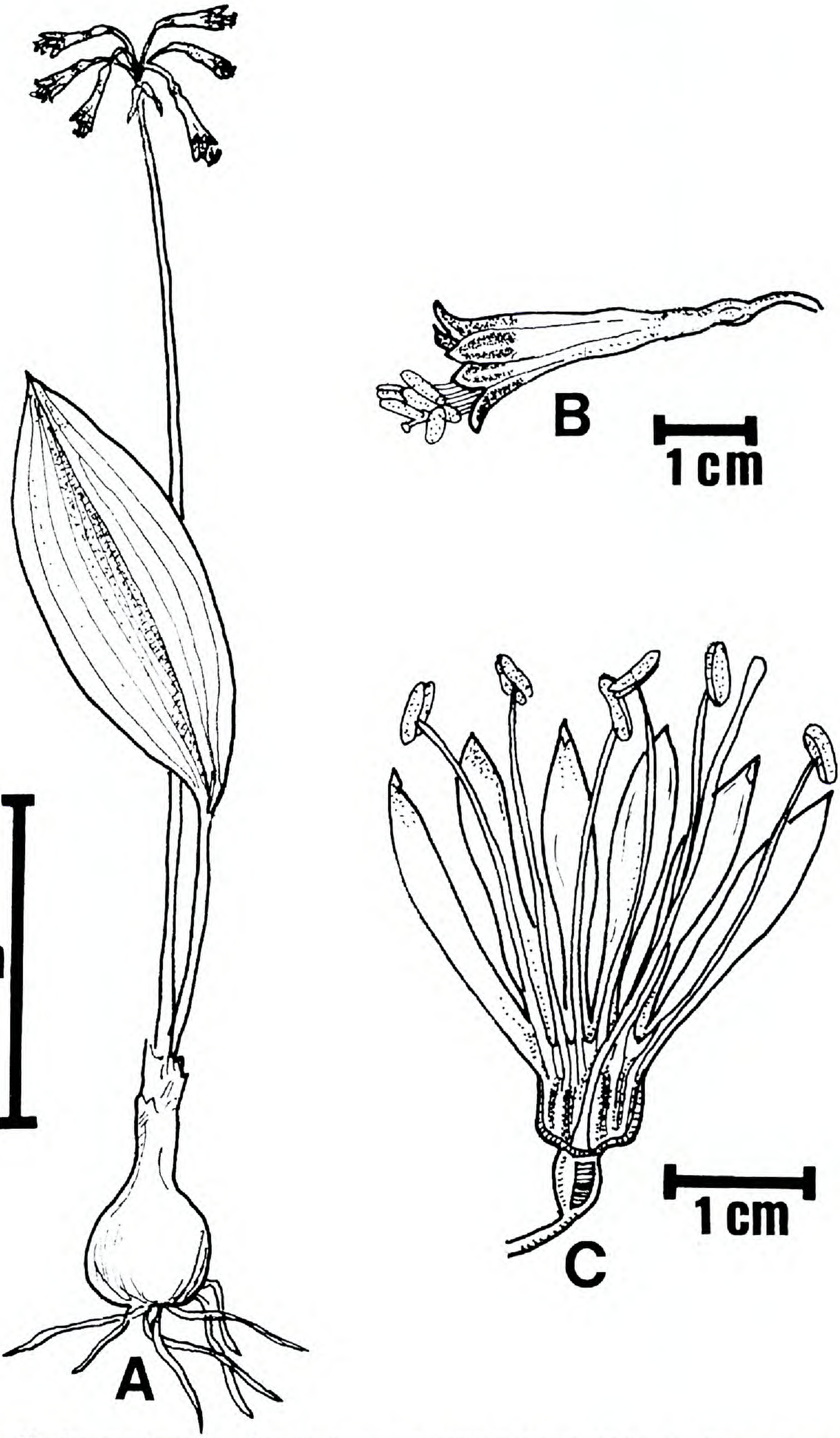


Figure 1. *Phaedranassa brevifolia*, after *Madison et al. 4958* (SEL). A. Habit. B. Flower, lateral longitudinal view. C. Flower, dissected.

straight or slightly cernuous; tepals concrescent for most of their length, spreading distally to 9 – 12 mm, lanceolate, rose-pink with a yellow adaxial stripe, the apices light green with a pink (outer tepals) or white (inner tepals) hyaline margin; outer tepals 31 – 32 mm long, 4 – 4.5 mm wide with a green apiculum; inner tepals 29 – 30 mm long, 5 – 5.5 mm wide, acute. Stamens six, proximally fasiculate and closing off the perianth throat, free, exserted 2 – 3 mm from the perianth; filaments biseriate, the 3 opposite the inner tepals ca 26 mm long, 3 opposite outer tepals ca 29 mm long, filiform, pink; anthers oblong, ca 5 mm long, dorsifixed and versatile, introrse. Style ca 43 mm long, filiform, pink; stigma capitate, minute, less than 1 mm wide. Ovary oblong-ellipsoid, 5.5 – 6 mm long, 2.2 – 3.5 mm wide, green; ovules ca 20 in each locule, axile, biseriate, compressed. Fruit and seed unknown.

TYPE: ECUADOR. IMBABURA: Tercer Paso, on the San Lorenzo River, dry thorn scrub, 1100 m, 7 Jun 1978, *Madison et al.* 4958 (HOLOTYPE: F!; ISOTYPE: SEL!).

Previously, only two species of *Phaedranassa*, *P. tunguraguae* and *P. cinerea*, have been described from elevations below 2000 m. *Phaedranassa brevifolia* differs from *P. cinerea* by its small, non-glaucous leaves, from *P. tunguraguae* by its smaller leaves and flowers, and from both previously described species by its markedly amphistomatic leaves (adaxial stomata are rare on leaves of both *P. cinerea* and *P. tunguraguae*), fewer and smaller flowers, lighter green tepal apices, yellow stripe on the tepals, pink margins of the outer tepals (yellow in both *P. cinerea* and *P. tunguraguae*), and pink filaments and style. The three species each have distinctive abaxial leaf surface morphology (Figures 2 – 4). *Phaedranassa brevifolia* is a plant of xeric thorn scrub; *P. tunguraguae* and *P. cinerea* occur in steep, locally dry, open situations in moist montane forest. Like *P. tunguraguae* (Meerow 1985; Ravenna 1969), *P. brevifolia* is known only from the type locality (Figure 8).

The somatic chromosome number of *P. brevifolia* is $2n = 46$ (Figures 5 – 7A, Table 1), as has been previously reported for the genus (Brandham and Durodie 1981; Snoad 1952). This number is characteristic of most Neotropical genera of Amaryllidaceae "infrafamily" Pancratioidinae (Di Fulvio 1973; Flory 1977; Meerow 1986, 1987).

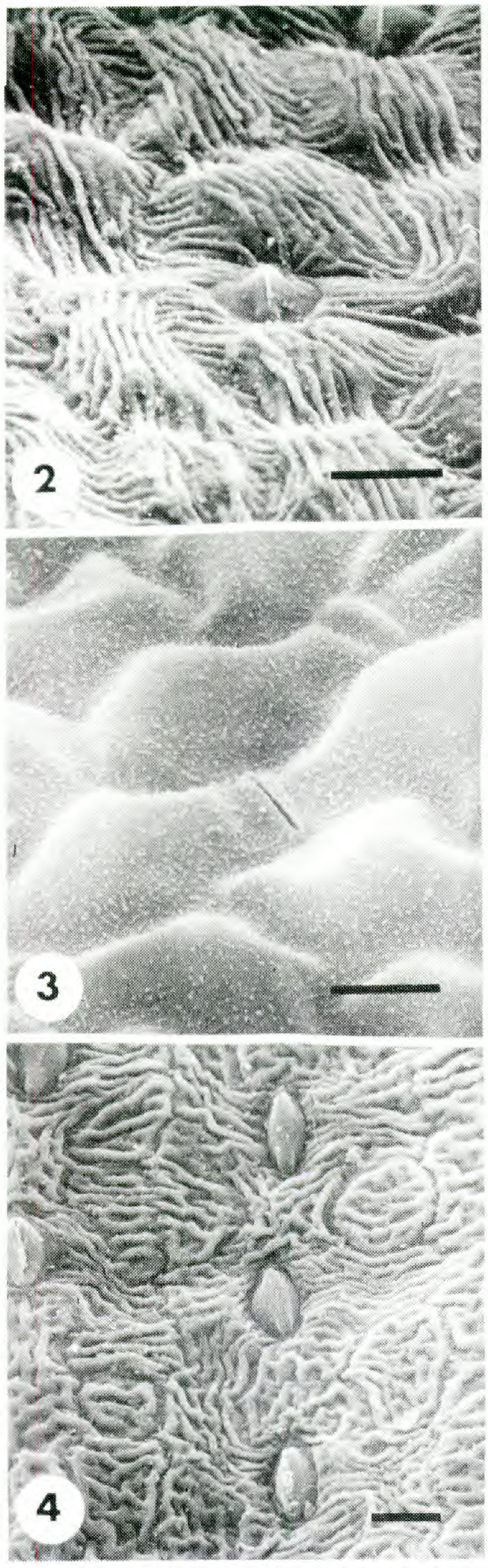
THREE NEW SPECIES OF EUCHARIS

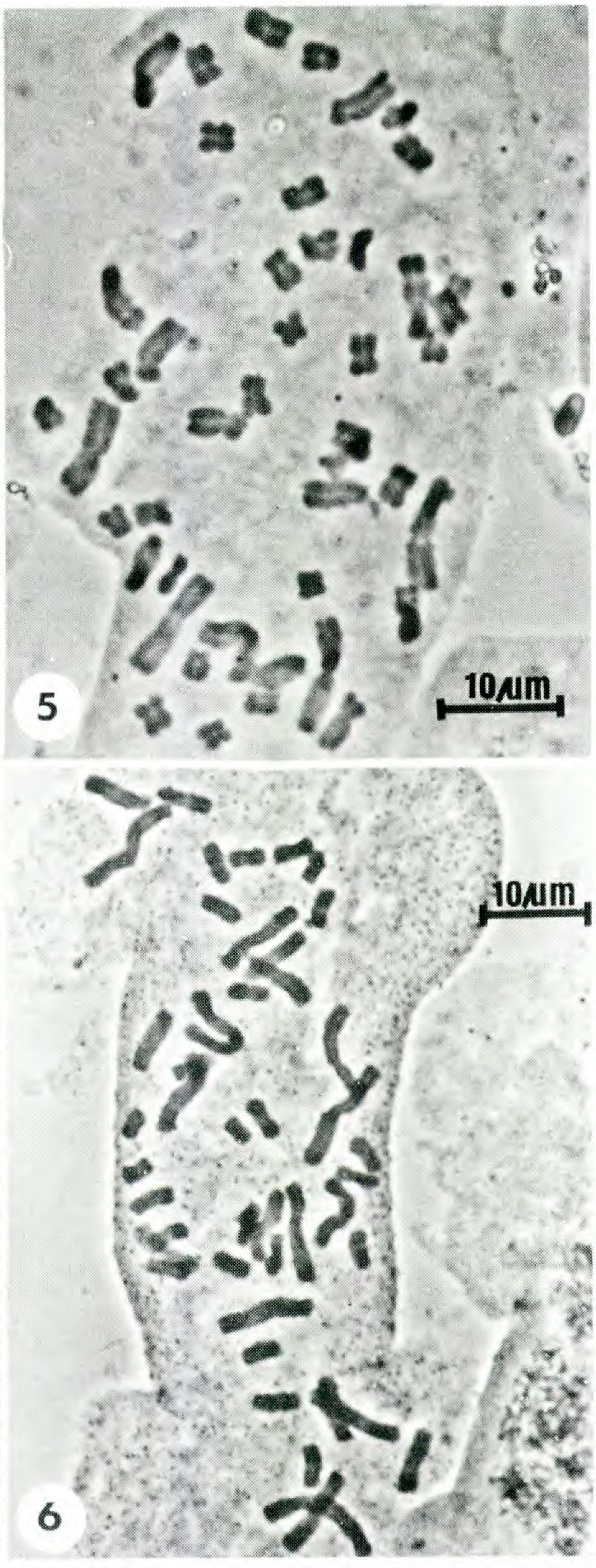
Eucharis is genus of 16 species ranging from Guatemala to Bolivia (Meerow 1986). The plants are found in the understory of primary, rarely secondary, rainforest, but only in edaphic situations of high fertility. The plants do not tolerate high light levels, and are not able to recolonize readi-

TABLE 1. Karyotype data, *Phaedranassa brevifolia*, *Eucharis moorei*, *E. cyaneosperma*, and *E. formosa*. All vouchers deposited at FLAS unless otherwise stated.

SPECIES, VOUCHER, 7 FIGURE NO.	2n	CHROMOSOME SIZE[a] RANGE (μm)	CHROMOSOME SIZE RANGE (relative length)[b]	CHROMOSOME SIZE[c] GROUPS L / ML / M / S	CHROMOSOME[d] MORPHOLOGY L / ML / M / S
Phaedranassa brevifolia (Madison et al. *4958*, SEL) Figures 5-7A	46	2.5 – 10.4 (±0.4) (±1.4)	2.4 – 10.0 (±0.3) (±0.8)	4 10 8 24	m: 2 4 nm: 2 2 20 sm: 8 2 st: 2
Eucharis moorei *(Meerow & Meerow 1141)* Figures 7B, 11	46	2.6 – 13.5 (±0.3) (±0.9)	1.9 – 10.1 (±0.2) (±0.7)	6 8 6 26	m: 2 nm: 4 2 18 sm: 6 4 4 st: 2 2 t: 2
E. cyaneosperma *(Meerow 1032)* Figures 7E, 12	46	3.y – 16.7 (±0.2) (±1.4)	2.2 – 9.6 (±0.2) (±0.3)	6 6 14 20	m: 2 2 6 nm: 2 2 6 6 sm: 2 2 6 8 st: 2
E. formosa *(Meerow 1099)* Figures 7C, 13	46	2.6 – 14.2 (±0.4) (±1.9)	1.9 – 10.6 (±0.3) (±0.8)	4 10 6 26	m: 2 6 nm: 2 10 sm: 6 4 10
E. formosa *(Schunke 14174)* Figures 7D, 14	46	2.6 – 13.1 (±0.5) (±1.5)	2.1 – 10.5 (±0.3) (±0.5)	6 6 10 24	m: 4 4 nm: 14 sm: 2 4 6 st: 6 6

[a]mean of five cells
[b]based on a value of 100 for the haploid complement; mean of five cells
[c]L = long, ML = moderately long, M = medium, S = small
[d]m = metacentric, nm = near-metacentric, sm = submetacentric, st = subtelocentric, t = telocentric





Figures 2 – 6. 2 – 4. Scanning electron photomicrographs of abaxial leaf surfaces of *Phaedranassa* species. Scale bars = 50 µm. 2. *P. brevifolia* (*Madison et al. 4958*, SEL). 3. *P. cinerea* (*Meerow & Meerow 1045*, FLAS). 4. *P. tunguraguae* (*Meerow & Meerow 1130*, FLAS). 5 – 6. Root tip mitotic metaphase configurations of *Phaedranassa brevifolia* (*Madison et al. 4958*, SEL), $2n = 46$. Two chromosomes are outside the frame of Fig. 5.

ly after disturbance of the forest canopy. Consequently, the species are often rare or widely dispersed. The greatest concentration of species is in western, lowland Amazonas and the adjacent foothills of the central Andes. Two subgenera are recognized in the most recent revision of the genus (Meerow 1986); *Eucharis* (13 species) and *Heterocharis* Meerow (3 species). *Caliphruria* Herbert is recognized as a distinct genus in this treatment.

EUCHARIS **moorei** (Baker) Meerow, stat. nov., (subg. *Heterocharis*; Figures 9A–C, 10A, B). *Eucharis grandiflora* Planch. & Linden var. *moorei* Baker, Gard. Chron. 4:628. 1888. TYPE: *ex hort Glasnevin*, no other data, 1888 (HOLOTYPE: K!).

Evergreen bulbous geophyte. Bulb 6–7 cm long, 2.5–4 cm diam., tunics brown. Leaves persistent, 2–3; petiole 2–4 dm long, 5–7 mm thick, with an anomalous arc of secondary vascular bundles near the adaxial surface; lamina broadly ovate, length/width ratio less than or equal to 2, 17–30 cm long, 10–14 cm wide, apex shortly acuminate, base appearing cordate at the margins, coarsely undulate, lustrous dark green adaxially, lighter green abaxially, abaxial cuticle mostly without striations. Inflorescence scapose, umbellate, terminated by two marcescent, valvate-imbricate bracts that enclose the flowers before anthesis; scape 5–7 dm tall, terete, 7–10 mm diam. proximally, ca 5 mm diam. distally; bracts ovate-lanceolate, (25–) 35–45 mm long, green. Flowers usually 4, rarely up to 7, more or less campanulate, declinate, sweetly fragrant; pedicels usually short, 3–10 (–18) mm long; tube 40–52 mm long, cylindrical and 1.7–2 mm wide proximally, abruptly dilating at about its midpoint to (15.5–) 18.5–25 mm at the throat, white except for a slight green tinge at the base; limb spreading less than 90° from the throat to ca 70 mm wide or less; tepals ovate, the margins undulate; outer series 3.3–4 cm long; 17 –22 mm wide, apiculate; inner series 2.9–3.8 cm long, 22–27 mm wide, obtuse. Stamens 6, connate into a conspicuous staminal cup; cup cylindrical, (8–) 10–15 (–16.4) mm long (to apex of teeth), 20 –25 mm wide, strongly recurved at the margins, white on the exterior, yellowish-green on the interior, shallowly and bidentate between each free filament, teeth acute, 2.5–3 mm long; each stamen ca 7–8 mm wide tooth-to-tooth; free filament subulate, (5–) 6–8.5 mm long, 2 mm or less at the base; anthers 5.5–6.5 mm long, oblong-linear, greyish-brown; pollen grain ca 48.6 × 71.2 μm. Style 6–7 cm long; stigma 2.5–3.5 mm wide. Ovary ellipsoid-trigonous, (7–) 10–13 mm long, ca 5 mm wide; ovules 16– 20, biseriate. Capsule globose, ca 1.5 cm long, 1.3 cm wide, slightly rostellate, green, slightly glaucous; seeds 1–3 per locule, compressed globose, ca 6 mm diam., turgid, testa blackish-brown and rugose. $2n = 46$ (Figure 7B, 11)

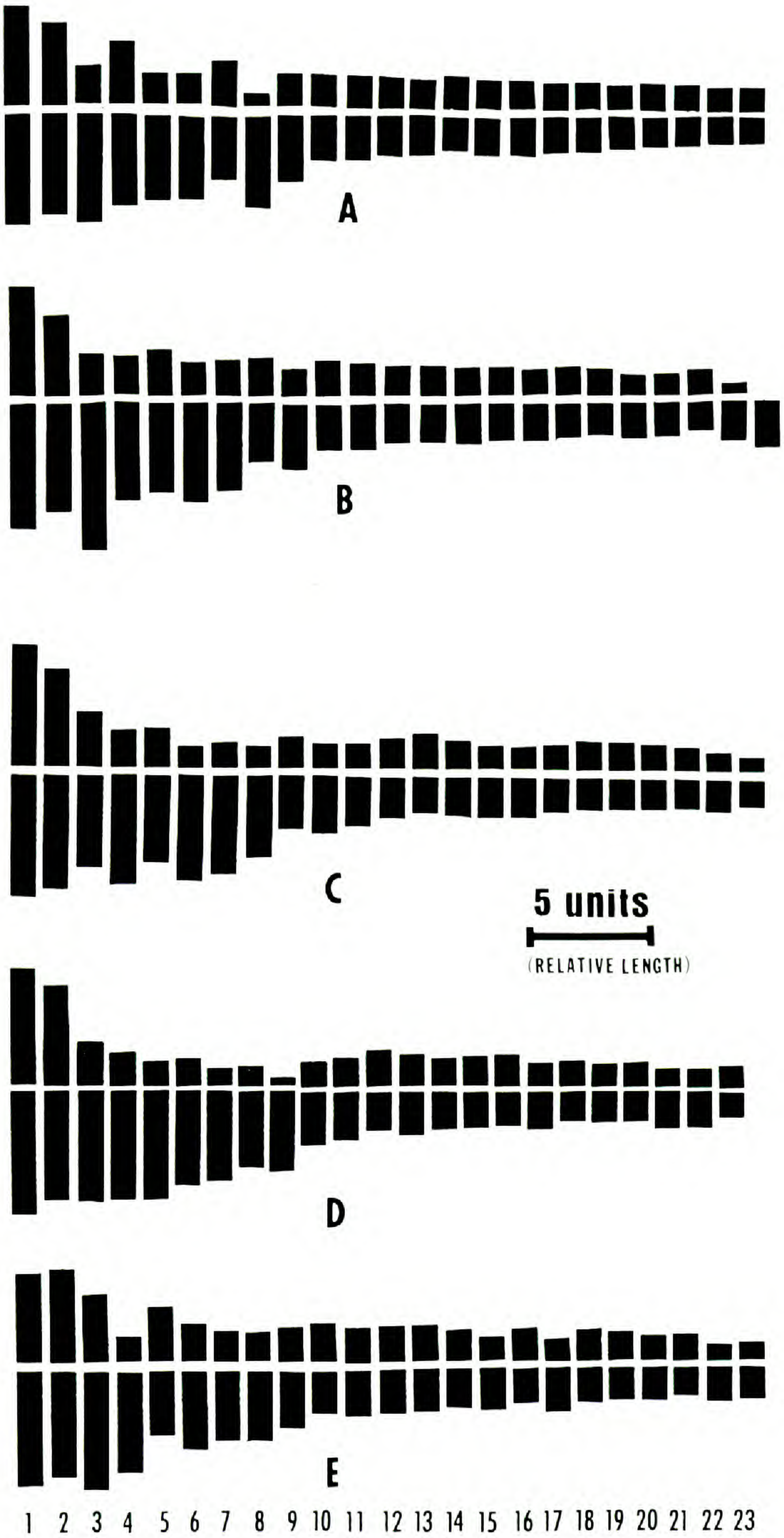


Figure 7. Haploid idiograms. A. *Phaedranassa brevifolia* (*Madison et al. 4958*). B. *Eucharis moorei* (*Meerow & Meerow 1141*, FLAS). C. *E. formosa* from Ecuador (*Meerow 1099*, FLAS). D. *E. formosa* from Peru (*Schunke 14174*, FLAS). E. *E. cyaneosperma* (*Meerow et al. 1032*, FLAS).

Distribution and ecology: An understory plant of primary and secondary lower montane rainforest of the Ecuadorean Andes, in Morona-Santiago and Santiago-Zamora Provences on the east slopes, and Los Rios, Cotopaxi and contiguous Pichincha Provences on the western declivity, (220 –) 600 – 1200 (– 2100) m; rare in the lower "ceja de montaña" of Cajamarca Department, Peru (Figure 15). Flowering is concentrated from January- – March and again from (June –) July – September.

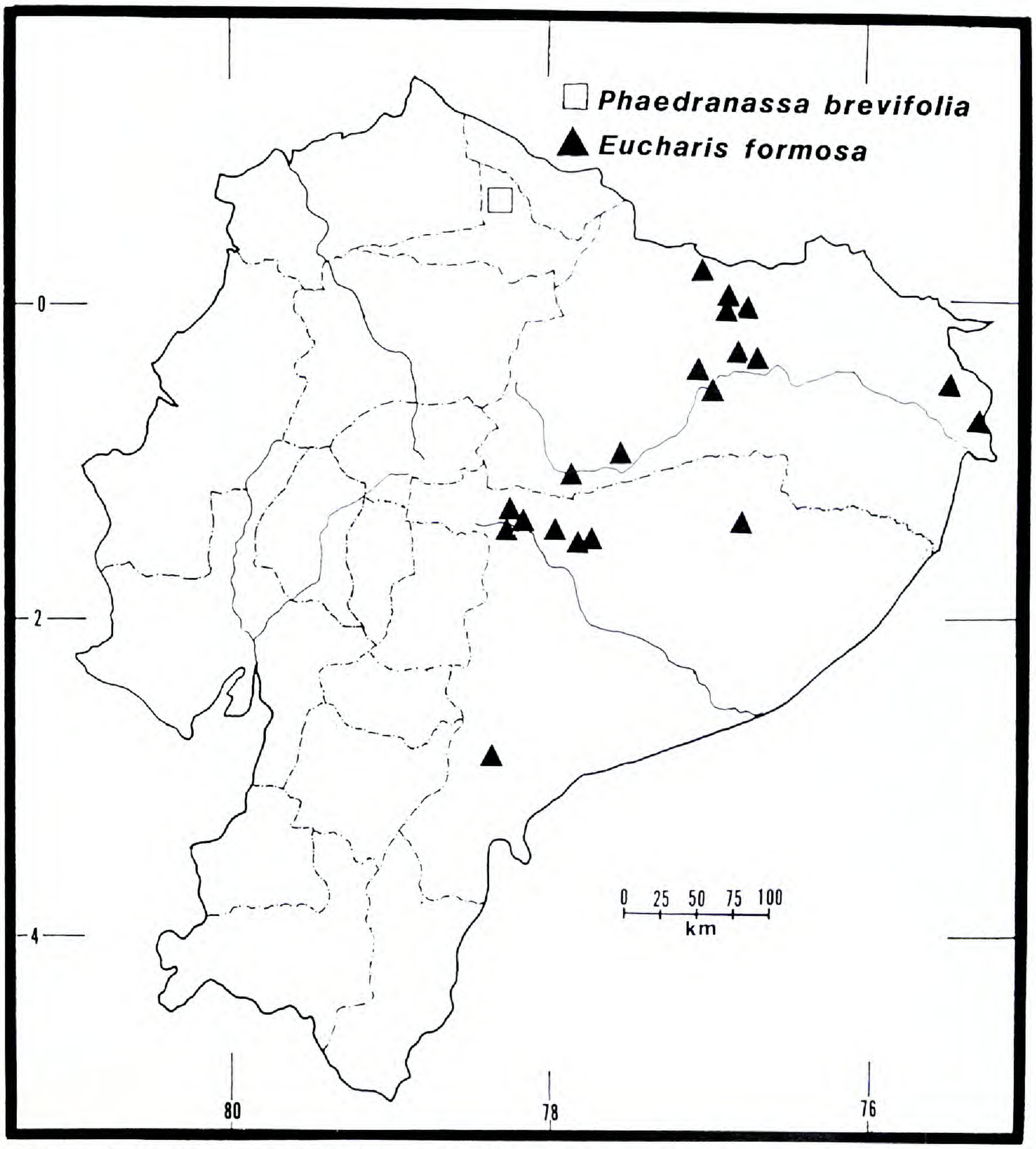


Figure 8. Distributions of *Phaedranassa brevifolia* and *Eucharis formosa* in Ecuador.

TABLE 2. Comparison of *Eucharis moorei* and *E. amazonica*.

CHARACTER	EUCHARIS MOOREI	EUCHARIS AMAZONICA
Leaf length/width ratio	< 2	> 2
Secondary petiolar bundles	conspicuous	reduced
Perianth morphology	campanulate	crateriform
Staminal cup dentation	acute	obtuse
Longest pollen grain equatorial diameter	71.2 μm	78.5 μm
Pollen stainability	100%	50 – 65%
Ovules per locule	16 – 20	9 – 12
Chromosome number ($2n$)	46	68
Distribution	Ecuador, on both sides of the Andes; rare in north central Peru	Peru, endemic to the middle Rio Huallaga valley

Additional material examined: ECUADOR. **Cotopaxi**: km 52 – 53 on rd from Quevedo to Latacunga, Río Pilalo, 800 – 950 m, 11 Aug 1984, *Meerow & Meerow 1137* (FLAS); same locality as preceding, 13 Aug 1984, *Meerow & Meerow 1141* (FLAS). **Los Rios**: km 56 Quevedo-Santo Domingo, Río Palenque Biological Station, 220 m, flowered in cultivation, *Dodson 5527* (SEL). **Morona-Santiago**: km 145, Cuenca-Gualaquiza, 1300 m, Jul 1982, *Dodson & Embree 13200* (MO, SEL); 27 km SE of San Juan Bosco, 1270 m, 27 Jan 1981, *Gentry et al. 30913* (MO, SEL); Indanza-Limón (General Plaza), 1300 – 1600 m, 23 Mar 1974, *Harling & Andersson 12779* (GB); Río Yunganza, rd Limón-Mendez (79°19′W, 2°49′S), 1100 m, 23 Sep 1979, *Holm-Nielsen et al. 20393 & 20407* (AAU); Río Gualaquiza and Río Bomboiza, east Andes of Sigsig, 800 – 1200 m, *Lehmann 5882* (K); 10 – 20 km from Gualaquiza on rd to Sigsig-Cuenca, 1300 m, 5 Aug 1984 *Meerow & Meerow 1135* (FLAS). **Pichincha**: Nanegal, west slope Andes, 5000 ft. *Jameson 9* (G, P). **Santiago-Zamura**: Yurupaza, 600 m, 3 Jun 1947, *Harling 1407* (GB); west side Río Valladolid, 2100 – 2400 m, 15 Oct 1943, *Steyermark 54717* (F). PERU. **Cajamarca**: Jaen, Río Tabaconas valley, 900 – 1000 m, May 1912, *Weberbauer 6251* (GH, US).

Herbarium material of *E. moorei*, when first received, was assigned to *E. amazonica* (Figures 10C, D). In 1984, I collected the species on both sides of the Ecuadorean Andes. Morphological and karyological differences between these collections and the Peruvian *E. amazonica* became evident (Table 2). *Eucharis moorei* is fully fertile, diploid ($2n = 46$) and of fairly wide distribution throughout Ecuador. An anomalous arc of secondary bundles appears in petiolar transverse sections of *E. moorei* and, reduced, in *E. amazonica* (Meerow 1986). These bundles are not found in any other species of the genus investigated. *Eucharis moorei* is putatively the most primitive species of the genus (Meerow 1986), with the greatest number of plesiomorphic character states in common with other genera of "infrafamily" Pancratioidinae (e.g., large, fragrant flower, short pedicels,

numerous ovules per locule). It is also one of only two *Eucharis* species that have telocentric chromosomes [Figure 7B, 11; the other species with telocentrics is *E. castelnaeana* (Baillon) Macbride of subg. *Eucharis* (Meerow 1986)]. Perianth and ovarian morphology of *E. moorei* is characteristic of *Eucharis* subg. *Heterocharis* Meerow, but the species has a conspicuous, long-exserted staminal cup as is characteristic of subg. *Eucharis*. The species also occupies a geographical position intermediate between *E. sanderi* (subg. *Heterocharis*), which is endemic to Chocó Department, Colombia, and the vast majority of subg. *Eucharis*. Species of subg. *Eucharis* are exceedingly rare on the western slopes of the Andes (Meerow 1986). *Eucharis moorei* is the only species in the genus that occurs on both sides of the Andes.

The presence of *E. moorei* in northwestern Ecuador, and the existence of putative natural hybrids between it and *E. sanderi* (*E.* × *grandiflora*) Planchon & Linden), might suggest that it was this plant which Planchon and Linden (1853) described as *E. grandiflora* from the Chocó region of Colombia. To date, however, I have not seen a single collection of *E. moorei* from Colombia. All material from Chocó is referable to *E. sanderi* or the natural hybrid. Furthermore, the staminal cup of the flower illustrated in the lectotype of *E.* × *grandiflora* is clearly much shorter than that of *E. moorei*, and the general habit of the figured plant closely resembles *E.* × *grandiflora*.

EUCHARIS **cyaneosperma** Meerow, sp. nov. (subg. *Eucharis*, Figure 9C, D).

Species a *E. ulei* Kranzl. affinis sed differt foliis ellipticis brevioribus, tubo minus arcuato, et testa seminali cobaltina.

Evergreen bulbous geophyte. Bulb subglobose, 3 − 5 cm long, 3 − 3.5 cm diam., tunics light brown. Leaves 2 − 4, persistent; petiole (10 −) 15 − 30 (− 35) cm long, 5 − 6.5 mm thick; lamina (ovate-) elliptic, 18 − 25 (− 30) cm long, (6.5 −) 7 − 8 (− 12) cm wide, apically acute to shortly acuminate, attenuate at the base. Inflorescence scapose, umbellate, terminated by two marcescent, valvate-imbricate bracts that enclose the flowers before anthesis; scape (3 −) 4 − 5 (− 6.5) dm tall, 5 − 7 mm diam. proximally, 3 − 4 mm diam. distally; bracts ovate-lanceolate, (20 −) 27 − 35 mm long. Flowers (3 −) 5 (− 7), pendent, without fragrance; pedicels (10 −) 15 − 25) (− 28) mm long, ca 1.7 − 2 mm diam.; tube 3 − 4 cm long, 1.5 − 2 mm diam. for most of its length, dilating abruptly to 7 − 9 mm proximal to the throat, curved abruptly ca 5 mm above the ovary then more or less straight; outer tepals 23 − 28 (− 32) mm long, 8 − 10 (− 13) mm wide, ovate-lanceolate, apiculate; inner tepals 21 − 24

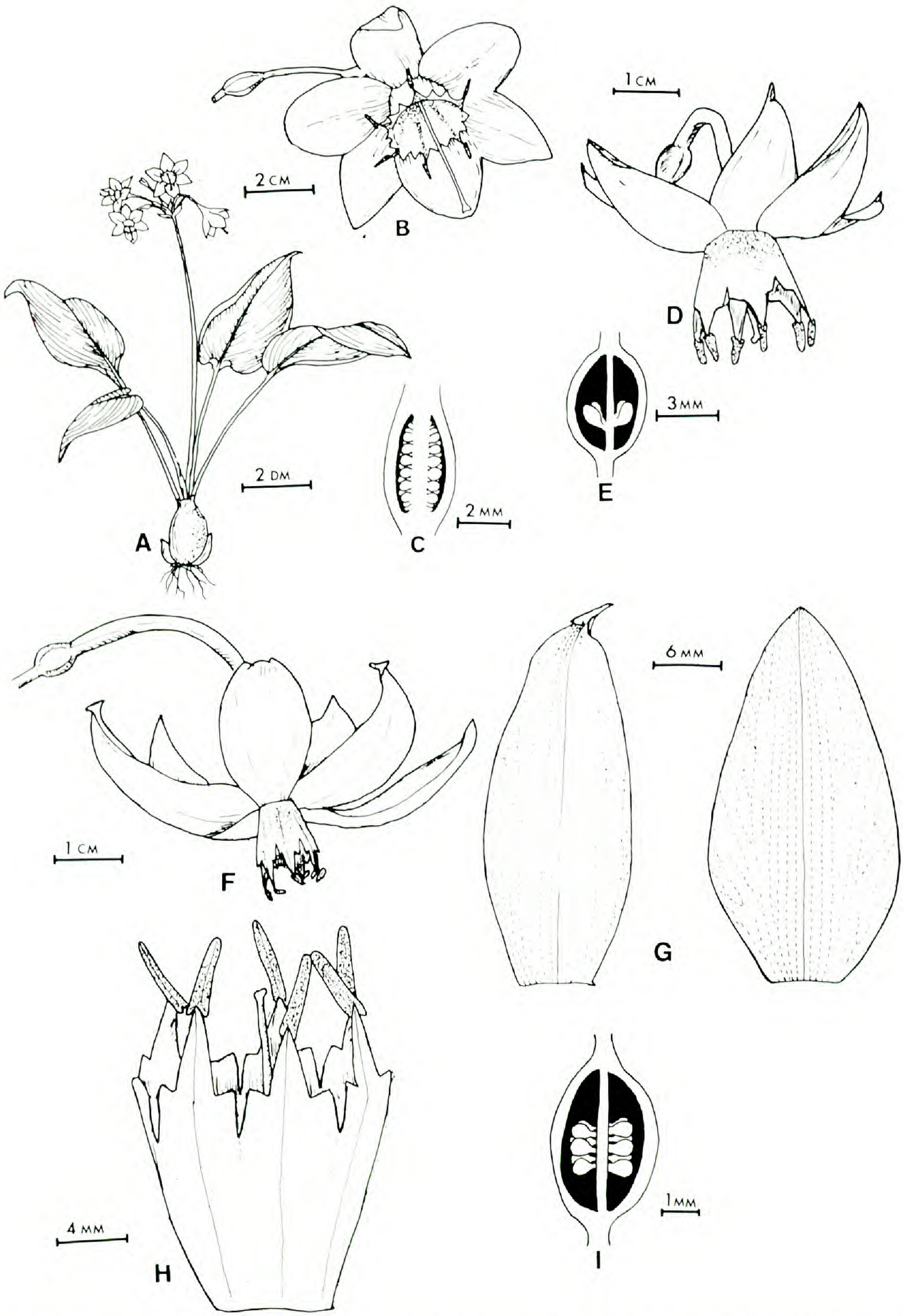


Figure 9. *Eucharis* species. A – C. *E. moorei* (after a drawing by Wendy B. Zomleffer of *Dodson* 5527, SEL). A. Habit. B. Flower. C. Longitudinal section of ovary. D – E. *E. cyaneosperma* (*Meerow 1032*, FLAS). D. Flower. E. Longitudinal section of ovary. F – I. *E. formosa* (*Meerow 1099*, FLAS). F. Flower. G. Tepals; outer (left), inner (right). H. Staminal cup. I. Longitudinal section of ovary.

(−30) mm long, 10−14 (−15) mm wide, ovate, acute to minutely apiculate. Staminal cup cylindrical, (8−) 10−12 mm long (to tooth or lobe), 10−13 (−15) mm wide, pale yellow or green in the proximal third, quadrate or irregularly toothed between each free filament, the teeth when present less than 1.5 mm long, cleft between each stamen 2−3 mm deep; each stamen 3.5−4 (−5) mm wide at the base; the narrow, subulate free filament (3−) 3.5−4.5 (−5.5) mm long, ca 1.5 mm wide at the base; anthers ca 3 mm long, oblong; pollen grain ca 47.95 × 67.55 μm. Style 4.5−6 cm long, exserted 0.5−1 cm beyond the anthers; stigma 2−2.5 mm wide. Ovary sub-globose-trigonous, 5−7 mm long, 7−10 mm wide, usually wider than long; ovules 2 (−3, 5) per locule, superposed in the lower half of the cell. Fruit a sub-globose, bright orange, leathery, triloculed, dehiscent capsule, 10−12 mm long, 15−20 mm wide; pedicel 25−36 mm long; seed ellipsoid, 7−9 mm long, ca 5 mm wide, with a lustrous, cobalt-blue testa. $2n = 46$ (Figure 7E, 12).

TYPE: PERU. SAN MARTÍN, 20 km north of Tocache Nuevo on road to Tarapoto, Río Cañuto, 520 m, 17 Jul 1982, *Meerow et al. 1032* (holotype: FLAS!).

Distribution and ecology: Rare in the understory of pre- to lower montane rainforest of the Amazon basin and eastern Andean foothills, from Peru to Bolivia, (330−) 400−800 (−1200) m elevation (Figure 15). Flowering at any time of the year but most commonly in August.

Additional material examined: BOLIVIA. **El Beni**: vicinity of Rurrenabague, 330 m, 25 Nov 1921, *Cardenas 1179* (AA, NY, US); Rurrenabague, 500 m, 7 Oct 1921, *Cardenas 1553A* (NY); San Antonio, 15 Nov 1958, flowered in cultivation 30 Apr 1959, *Nelson 58-301* (MO). BRAZIL. **Acre**: basin of Río Purus, near mouth of Río Macauhan, 9°20′S, 69°W, 17 Aug 1933, *Krukoff 5573* (NY); Río Branco de Obidos, Santo Antonio, 6 Aug 1912, *Ducke 12162* (GOEL, photo and fragment F). Amazonas: **Jurua Miry,** Jun 1901, *Ule 5737b* (B). PERU. **Cuzco**: Río Araza, northeast of Cuzco, 1150 m, Jan 1943, *Sandeman 3724* (K, OXF). **Loreto**: lower Rio Nanay, 24 May 1929, *Williams 431* [in fruit] (F); La Victoria on Amazon, 21 Aug 1929, *Williams 2619* [in fruit] (F); La Victoria on Amazon, 28 Aug 1929, *Williams 2878* [in fruit] (F, US). **Junin**: Puerto Yessup, ca 400 m, 10−12 Jul 1929, *Killip & Smith 26394* [in fruit] (F, NY, US); Río Negro to Satip, 800 m, 17 Aug 1960, *Woytkowski 5830* (MO). **San Martin**: *Schunke 4843* [in fruit] (F, US); Mariscal Caceres, Tocache Nuevo, Quebrada de Huaguisha, margen derecha del Río Huallaga, 400−450 m, 3 Jul 1974, *Schunke 7146* [in fruit] (F). **Ucayali**: middle Ucayali, Cashiboplaya, 10°S, 1923, *Tessman 3179* (G, NY, S).

Eucharis cyaneosperma is the only known species of *Eucharis* with blue-coated seeds. The species appears close to *E. ulei* in size, number of flowers, and ovule number, but differs by its usually shorter leaves, tube morphology, irregularly dentate to quadrate staminal cup (Figure 9C), and seed color. *Eucharis cyaneosperma* also occupies more upland sites than is usually characteristic of *E. ulei*. The species is nowhere abundant throughout its

Figure 10. A – B. *Eucharis moorei* (*Meerow & Meerow 1141*, FLAS). C – D. *E. amazonica* (*Schunke 14179*, FLAS).

broad range. Collections are concentrated in the southern end of the range of *E. cyaneosperma* (Figure 15), while *E. ulei* is more common to the north (Meerow 1986). The two species may represent sibling, allopatric divergences from a common ancestor that have since come into secondary contact.

EUCHARIS **formosa** Meerow, sp. nov. (subg. *Eucharis*, Figure 9F – I).

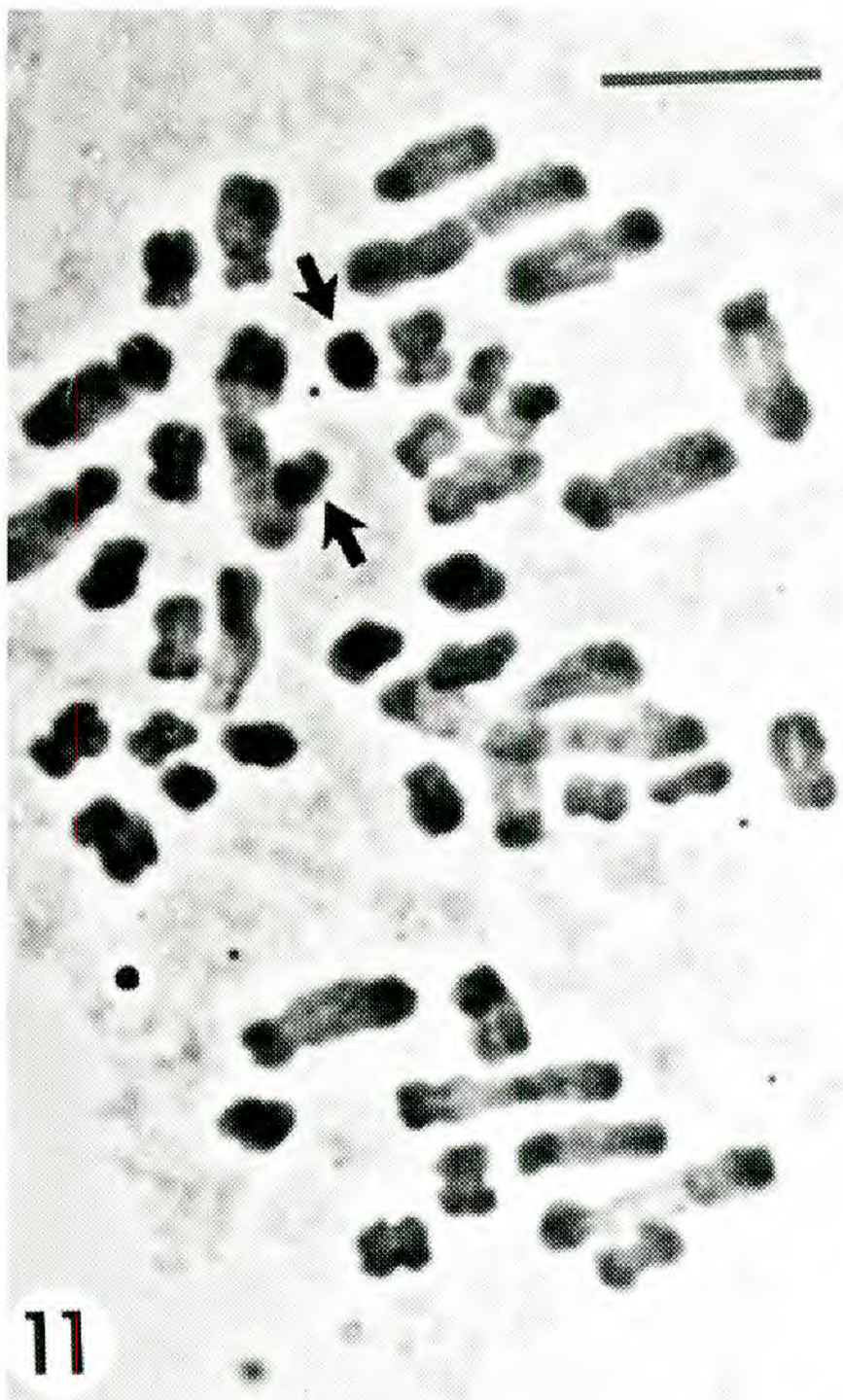
Eucharis candida Planchon et Linden primo adspectu maxime simile sed in omnes partes grandiores, floribus leniter fragrantibus, cupula staminea subcylindrica, et ovulis plerumque in quoque loculo plurimioribus; differt praecipue a *E. bakeriana* N.E. Brown cupula staminea angustiore inter stamina fissa profundius.

Evergreen bulbous geophyte to 6 – 8 dm tall. Bulb sub-globose, 4 – 7 cm long, 3 – 5 cm diam., neck 2 – 5 cm long, ca 1 cm thick, tunics brown. Leaves 1 – 2 (– 3), persistent; petiole 25 – 38 (– 42) cm long, 8.5 – 10 mm thick proximally, 5 – 6 mm thick distally; lamina elliptic, (21 –) 30 – 45 (– 52) cm long, (8 –) 11 – 15 (– 16) cm wide, usually conspicuously plicate, dark green and only slightly lustrous adaxially, light green abaxially, abaxial cuticle striate, margins coarsely undulate.

Inflorescence scapose, terminated by two marcescent, valvate-imbricate bracts; scape (5 –) 6 – 7 (– 8) dm tall, ca 1 cm diam. proximally, 5 – 6 mm diam. distally; bracts ovate-lanceolate, (36 –) 43 – 60 (– 85) mm long, 10 – 15 cm wide at the base. Flowers 8 – 10, very rarely less, pendent, emitting a mild, "sour" odor, crateriform; pedicels (8 –) 12 – 18 (– 30) mm long; tube 35 – 45 (– 50) mm long, ca 2 – 2.5 mm wide for most of its length, abruptly dilated to (9 –) 10 – 13 (– 14) mm at the throat; limb spreading to (55 –) 60 – 70 (– 80) cm; tepals sometimes recurved distally; outer tepals narrowly ovate, (30 –) 35 – 45 (– 47) mm long, (10 –) 15 – 18 (– 20) mm wide, apiculate, apiculum conspicuously horned adaxially (Ecuadorean populations); inner tepals ovate, (28 –) 32 – 40 (– 45) mm long, (15 –) 18 – 22 (– 25) mm wide, acute to minutely apiculate. Staminal cup funnelform-cylindrical, 10 – 13 (– 15) mm long (to apex of teeth or lobes), (15 –) 17 – 20 (– 22) mm wide; flushed greenish-yellow proximally, with the greatest concentration of pigment below each free filament, rarely only widely punctate; bidentate, irregularly toothed, lobed or quadrate between the distal portion of the filament; cup cleft between each stamen for 3 – 5 mm; teeth when present acute to obtuse, 2 mm or less long; each stamen (5 –) 6 – 7 (– 7.5) mm wide tooth-to-tooth or lobe-to-lobe; distal portion of filament subulate, (4.5 –) 5 – 6.6 (– 7) mm long, (1.8 –) 2 – 2.5 (– 3) mm wide at point of dilation; anthers oblong, 4.5 – 5.5 (– 6) mm long, grey-brown; pollen grain 47.7 – 53.4 × 65.5 – 73.8 μm. Style 5.5 – 6 (– 6.5) cm long, exserted ca 1 cm beyond the anthers; stigma ca 2 – 3 mm wide. Ovary globose-ellipsoid, 6 – 8.5 (– 10) mm long, (4.5 –) 5.5 – 7 (– 7.5) mm diam., green; ovules (2 – 3, 4 –) 5 – 7 (– 8). Fruit a sub-globose, bright orange, leathery, triloculed, dehiscent capsule, 1.5 – 2 cm long, 2 – 3 cm wide; pedicels 3 – 4 cm long; seeds (1 –) 2 – 4 per locule, ellipsoid, 8 – 10 mm long, 5 – 6 mm diam., with a lustrous, smooth black testa. $2n = 46$ (Figures 7C, D, 13, 14).

Distribution and ecology: Rich, moist soil in the understory of pre- and lower montane rainforest, chiefly in the Napo and Pastaza drainage of Ecuador (Figure 8); less frequent in Amazonian Peru and Colombia, the lower "ceja de montaña" of north central Peru, and upper Huallaga valley of Peru (Figure 15); rare in central Colombia [a single, poorly documentd collection (*Killip s.n.*, COL) from near Popayan may be of cultivated origin], 100 – 1800 m; flowering most commonly January – March. A poultice of the bulbs is used to treat tumors (*Lawesson et al. 39632*); vernacular names: *cebolla de la selva, sugkip*.

TYPE: ECUADOR, MORONA-SANTIAGO, Road Limon-Macas, ca km 20 from Límon, primary rain forest and rastrojos, 700 – 900 m, 26 Mar 1974, *Harling & Andersson 12915* (HOLOTYPE: GB!; ISOTYPE: FLAS!).



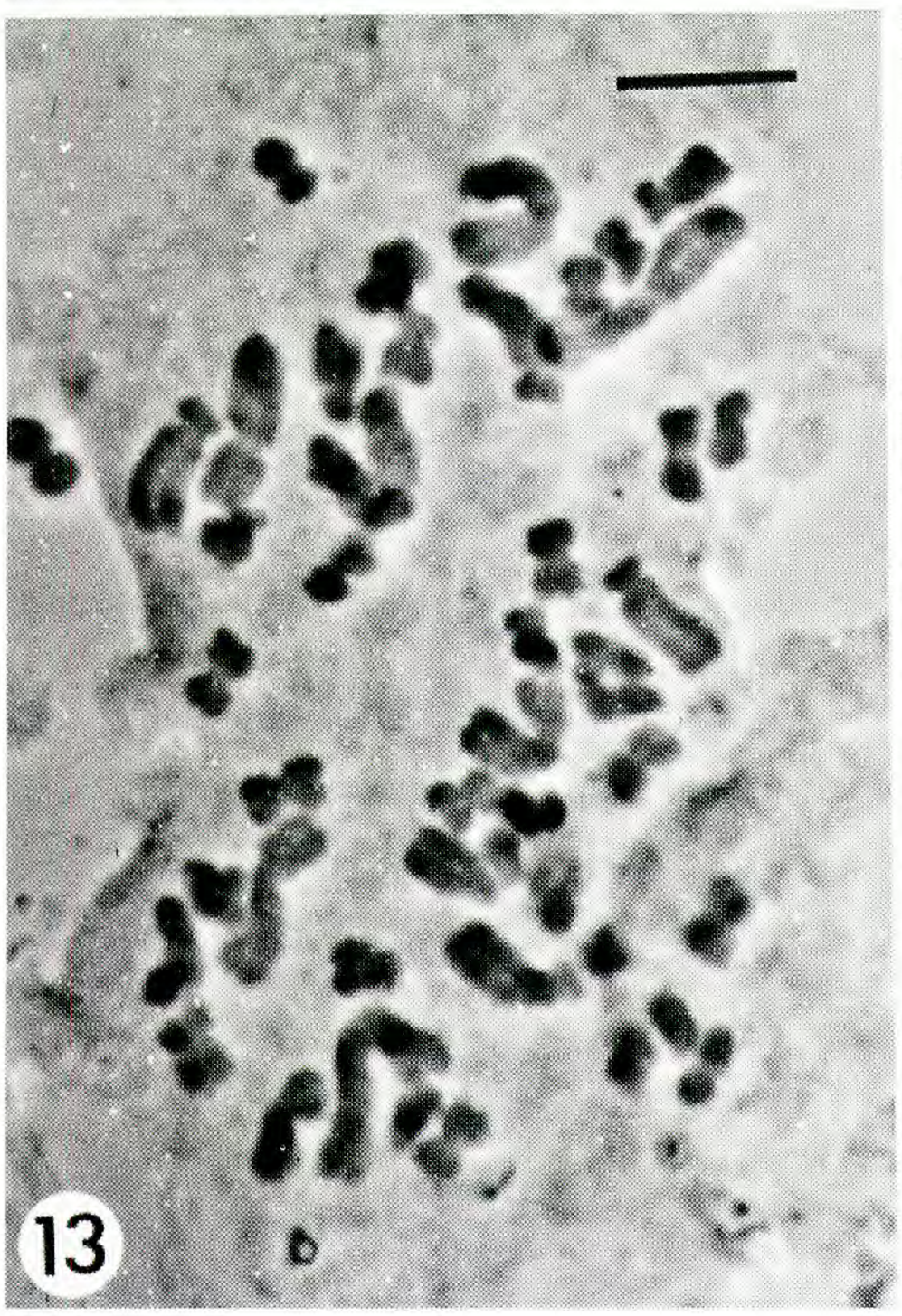


Figure 11 – 14. Root tip mitotic metaphase configurations of *Eucharis* species, all $2n = 46$. 11. *E. moorei* (*Meerow & Meerow 1141*, FLAS). Arrows indicate telocentric chromosomes. 12. *E. cyaneosperma* (*Meerow 1032*, FLAS). 13. *E. formosa* from Ecuador (*Meerow 1099*, FLAS). 14. *E. formosa* from Peru (*Schunke 14174*, FLAS). All scales = 10 μm.

Additional material examined: COLOMBIA. **Amazonas**: confluencia de los Ríos Amazonas y Loretoyacu, 12 Apr 1975, *Cabrera 3336* (COL); Trapecío amazonico, Loretoyacu River, ca 100 m, Sep 1946, *Schultes & Black 8342* [in fruit] (US); same locality as preceding, Oct 1946, *Schultes & Black 8410* [in fruit] (GH, US). **Caqueta**: Morelia, 150 m, 5 Oct 1941, *von Sneidern s.n.* (S). **Cauca**: Popayan, no other data, 25 Jan 1935, *Killip s.n.* (COL). ECUADOR: **Napo**: Napo, forest, 6 Oct 1939, *Asplund 9122* (S); Tena, marshy forest, 21 Oct 1939, *Asplund 9488* (S); Limoncocha, 300 m, 22 Jan 1977, *Dodson 6636* (SEL); 45 minute walk by trail from Santa Cecilia up Río Aguarico, ca 350 m, 28 Mar 1972, *Duyer & MacBryde 9699* [in fruit] (MO); Santa Cecilia, rainforest off runway, 340 m, 30 Mar 1972, *Duyer & Simmons 9743* [in fruit] (MO); Cañon de los Monos, ca 12 km north of Coca, 250 m, *Harling & Andersson 11719*, GB specimen (GB); path from Río Bueno to Santa Rosa, *Harling et al. 7201* (GB); Río Jivino, Limoncocha, 13 – 15 Mar 1968, *Harling et al. 7673* (FLAS, GB); Cañon de los Monos, road Coca-Lago Arrio, ca 12 km north of Coca, 24 Jan 1973, *Holguer 2960* (GB); Santa Cecilia, Lago Agrio-Baeza, ca 16 km west of Lago Agrio, 27 Feb 1973, *Holguer 3532* (FLAS, GB); Río Aguarico west of Detacamento Zancudo at entrance of Río Zancudo, 320 m, very rich soil, 29 Aug 1979, *Holm-Nielsen et al. 20168* [in fruit] (AAU); Añangu, Río Napo, 76°23′W, 0°32′S, 260 – 350 m, 27 Jun 1983, *Lawesson et al. 39632* (AAU); 4.2 – 7.5 km west of Lago Agrio (5 – 8.2 km east of Río Conejo) near Lago Agrio-Baeza Road, ca 340 m, 31 Mar 1972, *MacBryde & Duyer 1387* (MO); ex hort, voucher of SEL Acc. 78-1099, collected vicinity Limoncocha, 240 m, 15 Dec 1982, *Meerow 1103* (FLAS). **Pastaza**: Mera, ca 1100 m, 3 Mar 1956, *Asplund 19571* (S); Curaray (Jesús Pitishka), virgin rain forest near the posto militar, ca 200 m, 18 Mar 1980, *Harling & Andersson 17374* (FLAS, GB); between Nalpi and Canelo, 26 Feb 1971, *Holguer 1504* (FLAS, GB); trail from Indillama to Canelos, 400 m, occasional, 5 Feb 1935, *Mexia 6855* (UC, US); on Napo road north of Puyo, 16 Feb 1953, *Prescott 438* (NY). TUNGURAHUA: valley of Pastaza River, between Baños and Cashurco, 8 hours east of Baños, 1300 – 1800 m, *Hitchcock 21891* (GH, NY, US); vicinity of Río Margarjitas on Canelos trail, 1225 m, 19 Mar 1939, *Penland & Summers 142* (US). PERU. **Amazonas**: Quebrada Huampami, Lugar tseasim, monte al lado nayumpin, 800 ft, 3 Apr 1973, *Ancuash 161* (MO); Quebrada de apigkagentsa, Río Cenepa, 720 ft, *Kayap 597* (F, MO); Quebrada Cunup, monte cerca a la chacra, 800 – 850 ft, 24 Jul 1974, *Kayap 1298* [in fruit] (MO); Río Cenepa, vicinity of Huampami, ca 5 km east of Chávez Valdívia, ca 78°30′W, 4°30′S, Quebrada Aintami, 17 Aug 1978, *Kujikat 415* (MO). **Loreto**: Maynas, Yanamono, Explorama Tourist Camp, Río Amazonas, between Indiana and mouth of Río Napo, 72°48′W, 3°28′S, 120 m, 18 Aug 1980, *Gentry et al. 29867* (MO); same locality as preceding, 130 m, 18 Feb 1981, *Gentry et al. 31418* (MO); Maynas, Iquitos, Río Ampiyacu, 4 vueltas de Monona Cocha, 4 Aug 1976, *Revilla 990* (MO); Alto Amazonas, Yurimaguas, Camino a "Shunguyco," al sur-este de Puerto Arturo, cerca a Yurimaguas, 150 – 200 m, 1 Dec 1984, *Schunke 14157* (FLAS). **San Martín**: Mariscal Caceres, Tocache Nuevo, Camino a Shunté, 12 Mar 1970, *Schunke 3856* (F); Lamas, Alonso de Alvarado, Fundo Las Malvinas, carretera Moyobamba-Tarapoto, km 43, 850 m, 6 Dec 1984, *Schunke 14174* (FLAS).

Eucharis formosa is the most commonly encountered species in eastern Ecuador. It extends into Amazonian Peru and Colombia, and also occurs in the lower "ceja de montaña" forests of north central Peru. Like the closely related *E. candida*, *E. formosa* has a wide elevational range, though this may be in part the result of cultivation by transient agriculturists.

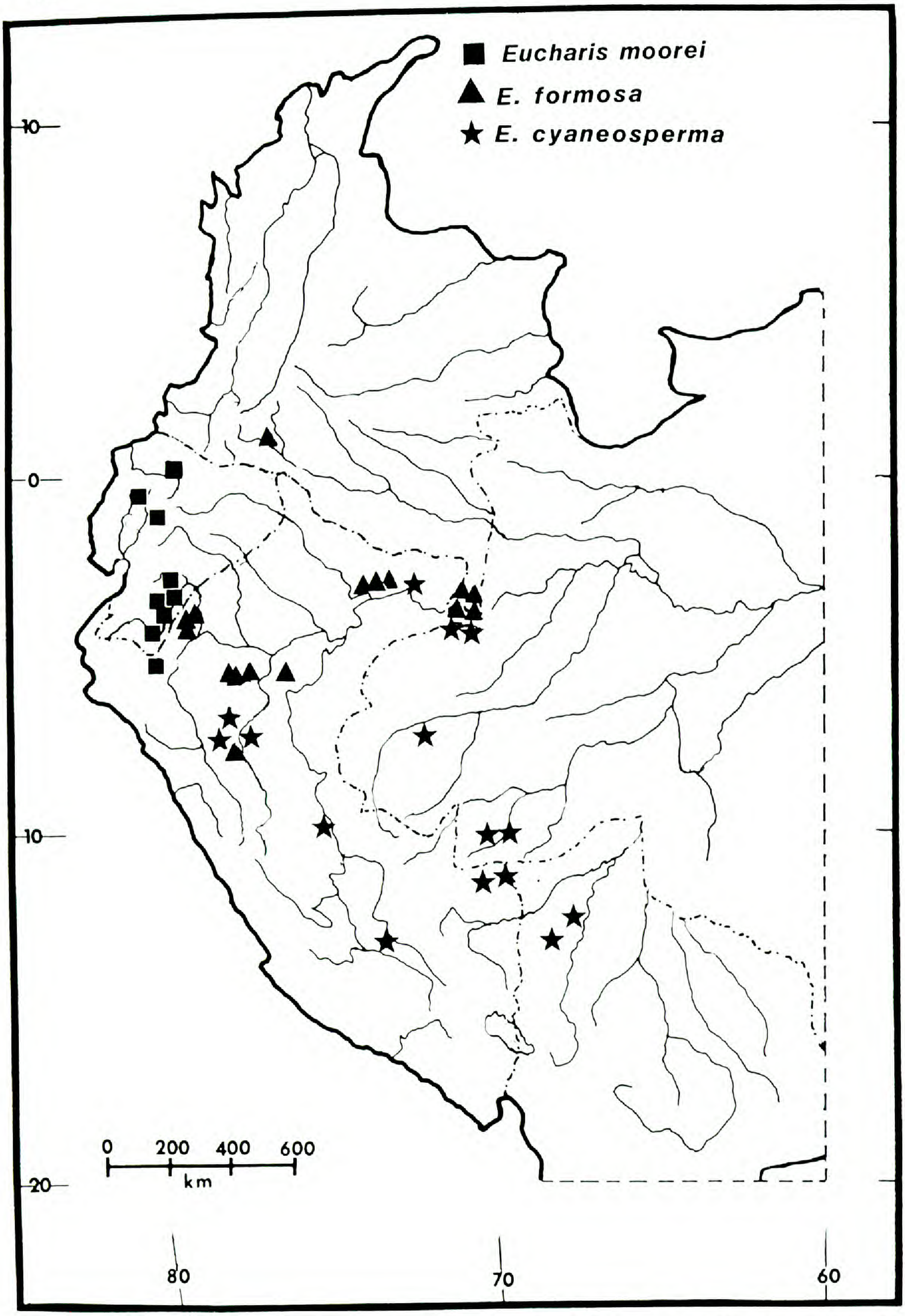


Figure 15. Distribution of *Eucharis moorei*, *E. cyaneosperma*, and *E. formosa* in northwest-central South America. See Figure 8 for Ecuadorean Populations of *E. formosa*.

Eucharis formosa is very often geographically sympatric with the smaller-flowered and less widely distributed *E. candida*. The species may be ecologically allopatric, however. Plants of *E. candida* which I collected in 1982 were growing along the bank of a small creek, just above the high water line. Populations of *E. formosa* were encountered in more upland sites. Nonetheless, in one instance two specimens (*Harling & Andersson 11719*), one each of the two species, were collected under the same number. To date, no species of *Eucharis* other than these two have been collected north of the Pastaza valley in eastern Ecuador. On the basis of herbarium study alone, Ecuadorean populations of these two taxa form a mosaic that seemed taxonomically insoluble until living material of both species from several populations was collected and flowered. Principal component analysis (Meerow 1986) supports recognition of these taxa as distinct species, and also suggest that *E. candida* and *E. formosa* have successfully hybridized in at least one area of sympatry. Nonetheless, the two entities appear phenetically distinct, and karyotype analysis (Meerow 1986) also supports the distinction between these closely related species. I believe the unprecedented degree of sympatry between these two species in Ecuador is inextricably related to their use by Indian people of the Napo and Pastaza basins. The bulbs are not only mashed for poultices, a general use to which many South American amaryllids are applied, but Indian women reportedly collect the plants quite actively for reasons they would not disclose (N. Whitten pers. comm.). Of course, aboriginal people are not without an aesthetic sense, and *Eucharis* have a pleasing aspect when in flower. Cultivation for ornamental as well as medicinal and ceremonial uses cannot be discounted. Most local inhabitants whom I met while collecting *Eucharis* in the Oriente were readily familiar with the plants when shown photographs. It is thus more than likely that both species have been transported about eastern Ecuador through human agency for years, if not centuries, perhaps even being transplanted from the wild into transient agricultural settlements. When these small gardens were abandoned after a few years, the bulbs probably recolonized locally. I am doubtful that even botanically astute native people would differentiate between such similar species as *E. candida* and *E. formosa*, and formerly allopatric populations may have been collected indiscriminently and cultivated together. Both species probably originated in the Napo-Pastaza drainage of Ecuador where present-day populations are now concentrated. *Eucharis formosa* is slightly better represented in the Pastaza valley than *E. candida*.

Eucharis formosa is larger in all parts than *E. candida*, and generally has more ovules per locule (though both species are quite variable in ovule number). The flowers of *E. formosa* emit a mild and not particularly

pleasant "sour" odor; flowers of *E. candida* are without noticeable fragrance. *Eucharis bakeriana*, a rare species from Peru, differs from *E. formosa* by its larger flowers, floral habit (perpendicular to the vertical scape axis), tube morphology (curved abruptly proximal to the ovary, then more or less straight), sweet floral fragrance, and plicate and shallowly cleft staminal cup. Karyotype and cladistic analyses indicate that *E. bakeriana* may have originated via rapid chromosomal change from sympatric populations of *E. formosa* in Peru (Meerow 1986).

Forms with toothed or edentate staminal cups occur throughout the range of *E. formosa* without any observable geographic pattern, as also occurs in *E. candida* and *E. ulei* Kränzlin (Meerow 1986). In cultivation, flowers of the same inflorescence can vary for this character. At least one Peruvian population (*Schunke 14174*) shows some karyotypic (Figures 7C, D, 13, 14) and allozyme divergence (Meerow 1986) from Ecuadorean populations. In floral morphology, however, it is indistinguishable from other collections.

ACKNOWLEDGMENTS

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HEXASTYLIS SHUTTLEWORTHII VAR. *HARPERI* (ARISTOLOCHIACEAE), A NEW VARIETY OF HEARTLEAF FROM ALABAMA AND GEORGIA

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ABSTRACT

Hexastylis shuttleworthii var. *harperi*, a new heartleaf from Alabama and Georgia, is described. Unlike *Hexastylis shuttleworthii* (Britten & Baker) Small var. *shuttleworthii*, *H. shuttleworthii* var. *harperi* has elongated and branched rhizomes, often forming a continuous ground cover in and around bogs where it is usually found. This heretofore undescribed variety is well-known in cultivation.

On June 5, 1927, in the swamp of Bridge Creek in Autauga County, Alabama, in the coastal plain, about a half mile from the type locality of *H. speciosa*, I found a few specimens of a *Hexastylis* with small cordate leaves, resembling *H. shuttleworthii*....

Roland Harper (1936) made these observations on an unidentified *Hexastylis* he had seen in 1927 at Bridge Creek swamp and in other "sour" non-alluvial swamps in the Coastal Plain of Alabama. He further pointed out that "... the plant usually grows in colonies connected by running rootstocks, and covering a few square feet, ..." Harper noted that flowers of the *Hexastylis* resembled those of *H. shuttleworthii* (Britten & Baker) Small. The flowers of plants Harper sent to F.V. Coville were identified as *H. memmingeri* (Ashe) Small [= *H. virginica* (L.) Small]; however, Harper (1936) determined that the flowers were intermediate in size between those of the latter taxon and those of *H. shuttleworthii*. Still unsure of the identity of the *Hexastylis*, Harper revisited the Bridge Creek population and another "swamp" population in Marion County, Alabama in 1935. Although he noticed considerable variation in flower size among the two populations, he finally concluded that the plant must be *H. shuttleworthii* (Harper 1936). The Alabama Coastal Plain populations of *H. shuttleworthii* were not mentioned again in the literature until 1945. In describing *Hexastylis pilosiflora* (Fern.) Blomq. & Oosting, Blomquist (1945) cited Harper (1936) and noted that Harper's plant could be an undescribed species closely related to *H. lewisii* (Fern.) Blomq. & Oosting, a species which occurs in the Piedmont and Coastal Plain of Virginia and North Carolina. Like *H. lewisii*, Harper's plant had "elongate rhizomes."

SIDA 12(1): 51 – 56. 1987.

Blomquist did not then propose, as did Harper (1936) earlier, that the Alabama plants were *H. shuttleworthii* (Blomquist 1945). In a subsequent revision of *Hexastylis*, Blomquist (1957) placed his *H. pilosiflora* in synonymy with *H. lewisii*; he did not mention Harper's bog *Hexastylis* per se, but apparently included Harper's Coastal Plain specimens under *H. shuttleworthii*. He pointed out that *H. shuttleworthii* occurred along the "borders of boggy areas" near the southern limit of its range.

In 1982, while examining herbarium specimens for the taxonomic treatment of *Hexastylis* for the *Vascular Flora of the Southeastern United States*, I noticed several small-flowered specimens of *H. shuttleworthii* from Alabama. I did not pursue the matter further until I saw several specimens from Auburn University (AUA) with very small, cordate leaves and small flowers labelled *H. harperi* (no authority given) and *H. lewisii* (Fern.) Blomq. & Oosting. Discussions with Dr. John Freeman of Auburn University, Mrs. L.G. Smith of Birmingham, correspondence with Dr. Robert Kral of Vanderbilt University, and a re-reading of Harper's (1936) paper further piqued my interest in the bog heartleaf from Alabama. In 1984, I found a population of the bog heartleaf in the Piedmont of Georgia, and in 1985, John Freeman took me to several Alabama Coastal Plain populations of the taxon. In all populations, the plant grew in large clumps, as Harper (1936) had indicated, sometimes covering more than a square meter of ground. After examination of about 50 flowers from four populations, I could find no extrafloral or intrafloral characters that separated the plant from *H. shuttleworthii*. The flowers were usually smaller (15 – 25 mm long) than those of *H. shuttleworthii* (15 – 40 mm long), but occasionally large flowers were found in the four populations. The plant was different from *H. shuttleworthii* primarily in growth form. Most *Hexastylis* species, including typical *shuttleworthii*, have short rhizomes with several terminal leaves only (usually only one new leaf is produced per year). The shallow rhizomes of the bog heartleaf had leaves along their entire length. A closer examination revealed that the rhizomes of the bog plant were elongated and branched in a complex manner. It was evident from the rhizomes that, instead of flowering every year, some years the plant produced a new growth shoot at the point where the flower normally appears (Fig. 1). This may explain Harper's (1936) comment that in some years flowers of the bog heartleaf are difficult to find. This shoot develops into a new branch of the rhizome and eventually produces flowers and roots yet still remains attached to the primary rhizome. Some new rhizomes may break off and grow independently of the primary rhizome. After several years, with the addition of new rhizome branches, the annual leaf production of the bog heartleaf increases dramatically. Furthermore, the leaves of

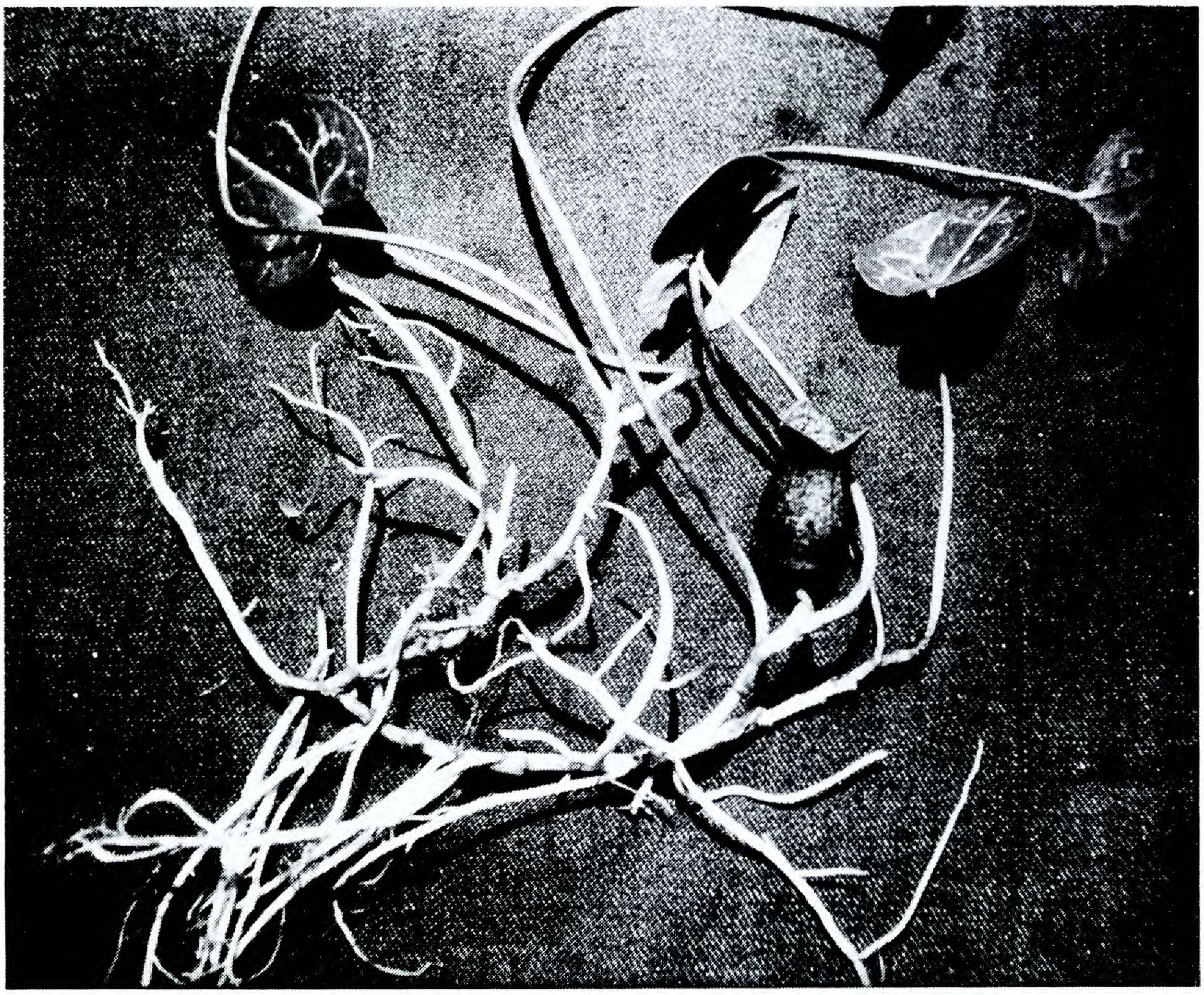

Figure 1. *Hexastylis shuttleworthii* var. *harperi*.

the bog *Hexastylis* often persist along the rhizome as do those of *H. lewisii* (Fernald 1943; Blomquist 1945). The many-branched rhizome and the persistent leaves give clumps of the plant the appearance of being large clones, although each clump is usually several interwoven individual rhizomes.

I concluded from my studies that the plant was either a variety of *H. shuttleworthii* or possibly only a modified growth form associated with boggy conditions. First in 1982 and then again in 1985, I examined several clumps of the bog *Hexastylis* that had been transplanted from a swamp in the Coastal Plain of Georgia (Webster County) to an upland situation in the University of Georgia Botanical Garden. In 1982, when it had only recently been transplanted, the plant seemed to be typical *H. shuttleworthii*, but with smaller flowers. (Young clumps of the bog heartleaf in Alabama populations are often indistinguishable from *H. shuttleworthii*.) By 1985, however, the transplanted clumps in Athens each covered nearly a square meter of ground; the rhizomes had begun to elongate and branch

and were producing leaves along the length of the rhizomes. The heartleaf thus retained its unusual growth form in an upland habitat. On the basis of diagnostic vegetative differences noted above, I am convinced that this taxon represents a new variety of *H. shuttleworthii* (Britten & Baker) Small and name this new variety in honor of Roland Harper, its original discoverer.

HEXASTYLIS SHUTTLEWORTHII (Britten & Baker) Small var. **harperi** Gaddy, var. nov. (Fig. 1)

A *H. shuttleworthio* rhizomatibus elongatis atque ramosis differt.

Variety *harperi* differs from var. *shuttleworthii* by its elongated and branched rhizomes, by its smaller (2.5 – 7 cm long and wide) orbicular to cordate-orbicular leaves, and by its smaller (15 – 25 mm long) flowers. Variety *harperi* may be separated from all other species of *Hexastylis* except *lewisii* by its growth form. The long white hairs on the inner surface of the calyx lobes of *H. lewisii* distinguish it from *H. shuttleworthii* var. *harperi*. Although clumps of plants are occasionally found in other species of *Hexastylis*, these clumps seem to be aggregated plants resulting from poor seed dispersal, rather than rhizome branching.

TYPE: UNITED STATES. GEORGIA. **Madison Co.**: acidic bog under *Acer rubrum*, *Liriodendron tulipifera*, and *Nyssa sylvatica* var. *biflora*. Growing on small hammocks with *Osmunda cinnamomea* and along bog edges with *Medeola virginiana* and *Isotria verticillata* just N of GA 106, 14.2 mi NE of Athens, 9 May 1986, *Gaddy s.n.* (HOLOTYPE: CLEMS; ISOTYPES: AUA, GA, GH, MO, NCU, NY, TENN, UNA, VDB).

Specimens examined: ALABAMA: **Autauga Co.**: swamp of Bridge Creek about 2 mi southeast of Booth, 15 Jun 1936, *R. Harper 3524*(GH, NY). **Chilton Co.**: rich mesophytic woods in seepage ravine S of U.S. Hwy 82, ca 0.5 mi E of its crossing of Big Mulberry Creek, ca 3 mi SSE of Maplesville, 20 May 1971, *J.D. Freeman 731* (AUA). **Macon Co.**: piney woods, 2 – 3 mi N of Tuskegee on U.S. 29 – turn right on dirt road at second bridge, 7 May 1971, *E.M. Tatum 151* (AUA). **Marion Co.**: drier spots in non-alluvial swamp west of Guin, 3 Jun 1936, *R. Harper 3515* (GH). **Perry Co.**: rich woods on mesophytic slope, 6 mi NW of Selma at tributary to Oakmulgee Creek, 1.5 mi W of creek, 3 May 1977, *A. Sessler, J.D. Freeman, & H.D. Moore 1221a* (AUA). GEORGIA: **Sumter Co.**: 1 mi S of Americus, small non-alluvial swamp, 20 Mar 1949, *R.F. Thorne & W.C. Muenscher 9012* (GH, CU). **Webster Co.**: Kinchafoonee Creek floodplain along U.S. 280, near Pearson, 22 Apr 1981, *A. Tate & R. Allen s.n.* (GA).

In 1984, Mrs. L.G. Smith directed my attention to a paper by (Galle 1984). Galle described moving several clumps of a "stoloniferous" *Hexastylis* from a private garden in Decatur, Georgia to Calloway Gardens in Pine Mountain, Georgia. Mr. Galle concluded that the plant was a form of *H. shuttleworthii* and proposed it be called *H. shuttleworthii* "Calloway." After examining Galle's description, the illustrations in his paper, and live material from Calloway Gardens, I have concluded that the "Calloway"

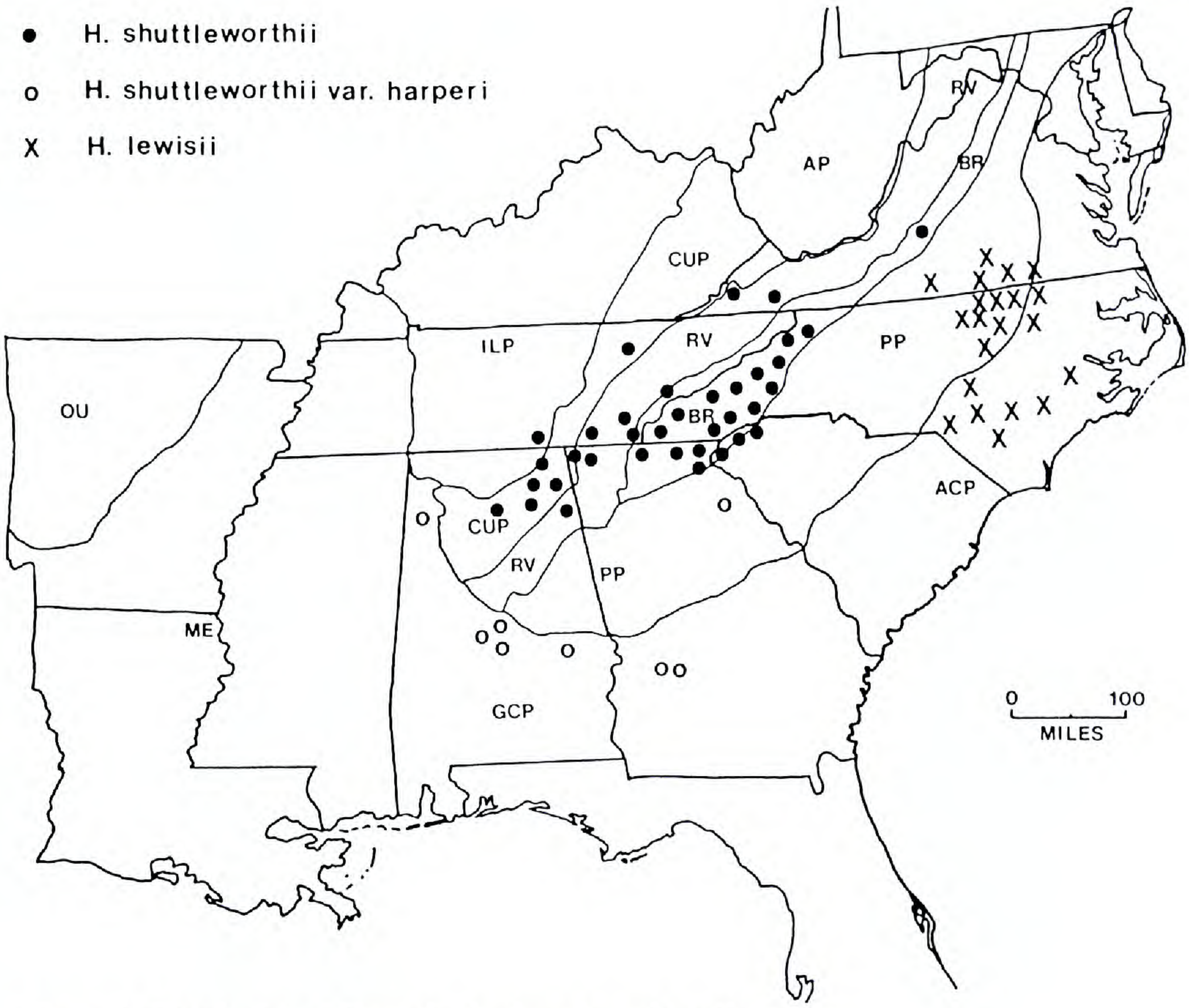

Figure 2. Distribution of *Hexastylis shuttleworthii* and its allies.

ginger is *H. shuttleworthii* var. *harperi*. The plant is very hardy in cultivation, having been successfully grown in several eastern states (Galle 1984). In fact, var. *harperi* may be more common in cultivation than in the wild. Unfortunately, the original source of the plants now growing in Calloway Gardens is unknown (Galle 1984).

ACKNOWLEDGMENTS

I would like to dedicate this paper to John Freeman of Auburn University and to Mrs. L.G. Smith of Birmingham, Alabama for their assistance and for their interest in the *Hexastylis* of Alabama. I would also like to thank Ms. Nancy Coile of the University of Georgia for pointing out the existence of the Webster County, Georgia specimens of *Hexastylis shuttleworthii* var. *harperi* and for directing my attention to live Webster County material in the University of Georgia Botanical Garden. I wrote this paper under support from the Hesler Endowment Fund while a Visiting Professor of Floristic Botany in the Department of Botany, The University of Tennessee, Knoxville.

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RANUNCULUS SECTION *ECHINELLA* (RANUNCULACEAE) IN THE SOUTHEASTERN UNITED STATES

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ABSTRACT

As highlighted by the SEM, surficial sculpturings of the achenes of seven species of *Ranunculus* section *Echinella* adventive within the southeastern United States show two species with incurved trichomes and five species with protuberances and spines of varying lengths and frequency. A key, descriptions, habitats, and ranges within the southeastern United States of the seven species are included.

INTRODUCTION

During an extensive study of the Ranunculaceae for the forthcoming volume 2 of the *Vascular Flora of the Southeastern United States*, it became increasingly apparent that members of the echinate group of *Ranunculus* were frequently misdetermined. This is due chiefly to the lack of a comprehensive treatment of these seven species, all naturalized from Europe or South America. Small's *Manual* (Small 1933) included only three species (*R. muricatus*, *R. parviflorus*, and *R. sardous* as *R. parvulus*), Radford (1968) treated four species (*R. arvensis*, *R. muricatus*, *R. parviflorus*, and *R. sardous*), while Benson (1948, 1954) described six species in his exhaustive review of the North American Ranunculi. Moreover, some of the species (e.g., *R. platensis*, Keener, unpubl. research) appear to be migrating rapidly, and thus to aid in understanding the taxonomy of this somewhat weedy group, the following general treatment is offered.

Species of *Ranunculus* sect. *Echinella* are demarked chiefly by the sculpturings of the achene faces: small tubercles, spines, or recurved trichomes, and thus differ from all other species of *Ranunculus* within the southeastern United States. Moreover, all are annuals with yellow petals, divided or

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TABLE 1. Voucher specimens for the SEM study. All specimens are deposited at PAC.

1. RANUNCULUS ARVENSIS L. NORTH CAROLINA: Durham Co.: 2 mi NW of Durham, *Blomquist 16404* (Fig. 4C). LOUISIANA: Madison Parish: Willow Bayou Road, 0.3 mi N of U.S. 80, *Rich & Scurria 1817* (Fig. 4D).
2. R. MARGINATUS D'Urv. LOUISIANA: Caddo Parish: 10.5 mi S of Shreveport, *MacRoberts 2630* (Fig. 3A, B).
3. R. MURICATUS L. TEXAS: Brazos Co.: Pexter Park, College Station, *Gilmore 27* (Fig. 4A, B).
4. R. PARVIFLORUS L. NORTH CAROLINA: Chatham Co.: 3 mi N of Farrington, *Ables & Haesloop 53318* (Fig. 1A, B).
5. R. PLATENSIS Sprengel. NORTH CAROLINA: Durham Co.: Duke University, Durham, *Murphy & Hammel 732* (Fig. 1C, D).
6. R. SARDOUS Crantz. TENNESSEE: Montgomery Co.: 8 mi SW of Clarksville, *Chester 4030* (Fig. 2A). ARKANSAS: Clark Co.: Arkadelphia, *Demaree 69393* (Fig. 2B).
7. R. TRILOBUS Desf. LOUISIANA: St. Martin Parish: 4.2 mi W, 3.5 mi S of Butte La Rose, *Haynes 4666* (Fig. 2C, D).

lobed basal leaves, and as colonizers inhabit waste ground, fallow fields, roadside banks and ditches, low clearings, and streambanks.

MATERIALS AND METHODS

Herbarium specimens forming the basis of the taxonomic treatment were examined from ALU, DUKE, FLAS, FSU, GA, GH, LAF, LSUS, NCSC, NCU, NLU, NO, OSH, PAC, SMU, UNA, US, VPI, and WIS. Achenes used in the SEM study were taken from specimens deposited at PAC (Table 1).

Achenes were mounted on aluminum stubs using either double-sided transparent tape or silver-conductive adhesive, then coated with gold for four minutes using an ISI Carbon and Gold Sputterer. Specimens were observed and photographed (Agfa Pan 100 −35 mm film) with ISI Scanning Electron Microscope.

MICROMORPHOLOGY OF THE ACHENE SURFACE

Achenes within *Ranunculus* section *Echinella* exhibit surficial sculpturings ranging from simple trichomes to protuberances and spines of varying lengths (*see* Theobald et al. 1979, for a description and classification of trichomes). Although the terminology for referring to these sculpturings is by no means uniform, we are using "trichome" to indicate the short, more or less recurved unicellular hairs found on the achenes of *Ranunculus parviflorus* and *R. platensis*. All remaining species have multicellular protuberances or spines of varying lengths and acuteness. Occasionally, especially in *R. sardous*, these protuberances appear as papillate swellings, but the term papillate is better reserved for similarly shaped protuberances within single cells (Wilkinson 1979).

Consequently, we recognize two main types of achene micromorphology for critical taxonomic purposes: 1) simple trichomes, and 2) multicellular protuberances and spines of varying lengths (0.05 to ca 1.0 mm). Protuberances tend to be quite short and "papillate" in appearance under low light magnification, whereas spines are longer and appear to be more sharply pointed (cf. Figs. 2B, D and 4A – C). Accordingly, the achenes of each species are described in more detail below.

Fig. 1A, B. *Ranunculus parviflorus*. Trichomes simple, unicellular, recurved, to 0.12 mm long, attached basally to short multicellular conelike protuberances, less frequent on the achene margins.

Fig. 1C, D. *R. platensis*. Trichomes simple, unicellular, somewhat recurved, to 0.16 mm long, attached basally to slightly raised multicellular projections, less frequent on the achene margins.

Fig. 2A, B. *R. sardous*. Protuberances multicellular, present or absent; when present, usually occurring toward the margins of the achene face, conelike ("papillate" in appearance), short (to 0.05 mm long).

Fig. 2C, D. *R. trilobus*. Spines multicellular, conelike, to 0.16 mm long, absent on the achene margins.

Fig. 3A, B. *R. marginatus*. Ornamentation similar to *R. trilobus* except that the spines (to 0.17 mm long) can be absent or sparse in the central area of the achene face.

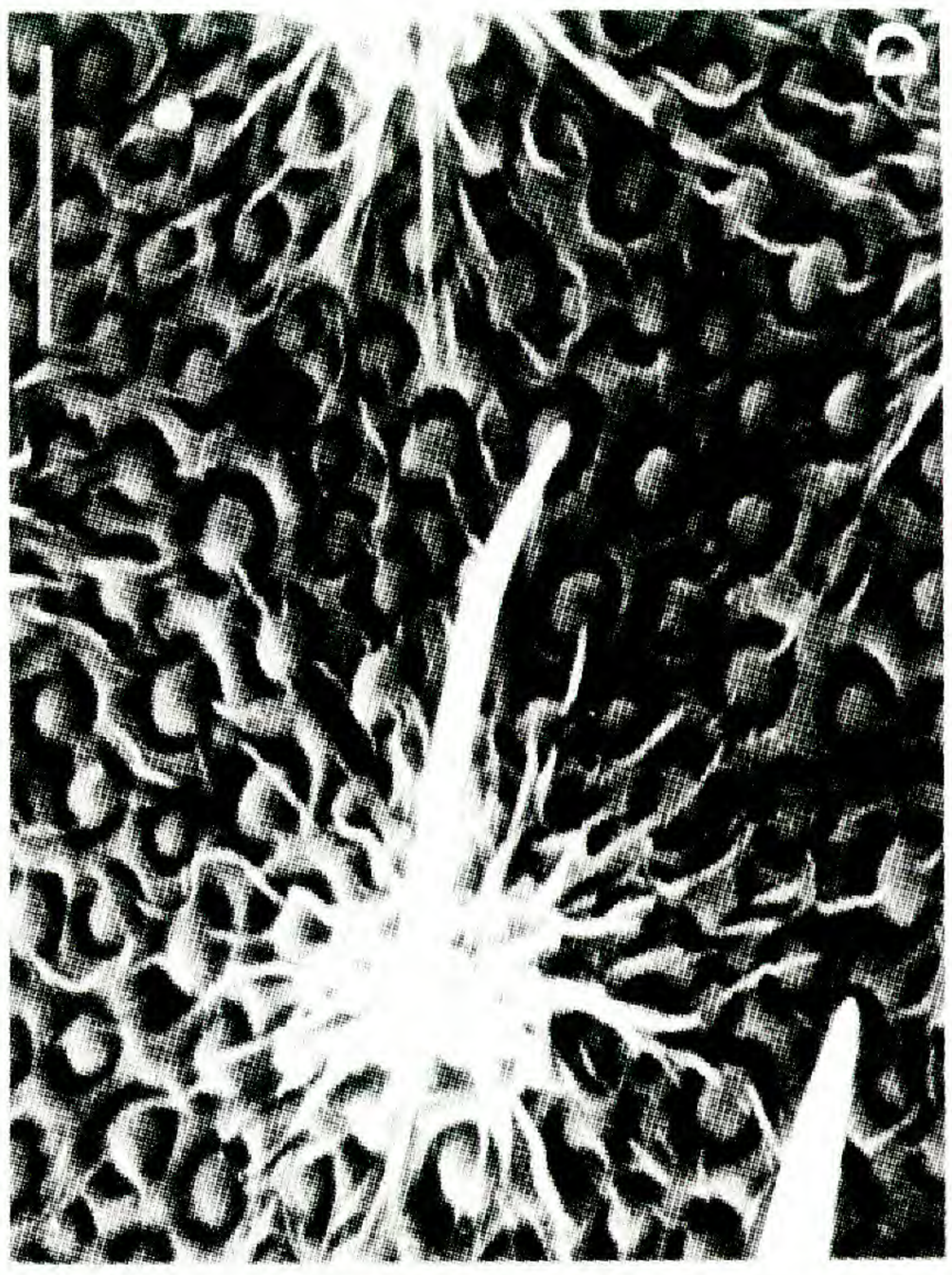
Fig. 4A, B. *R. muricatus*. Spines multicellular, conelike, to 0.60 mm long, with rough striations, absent on the achene margins.

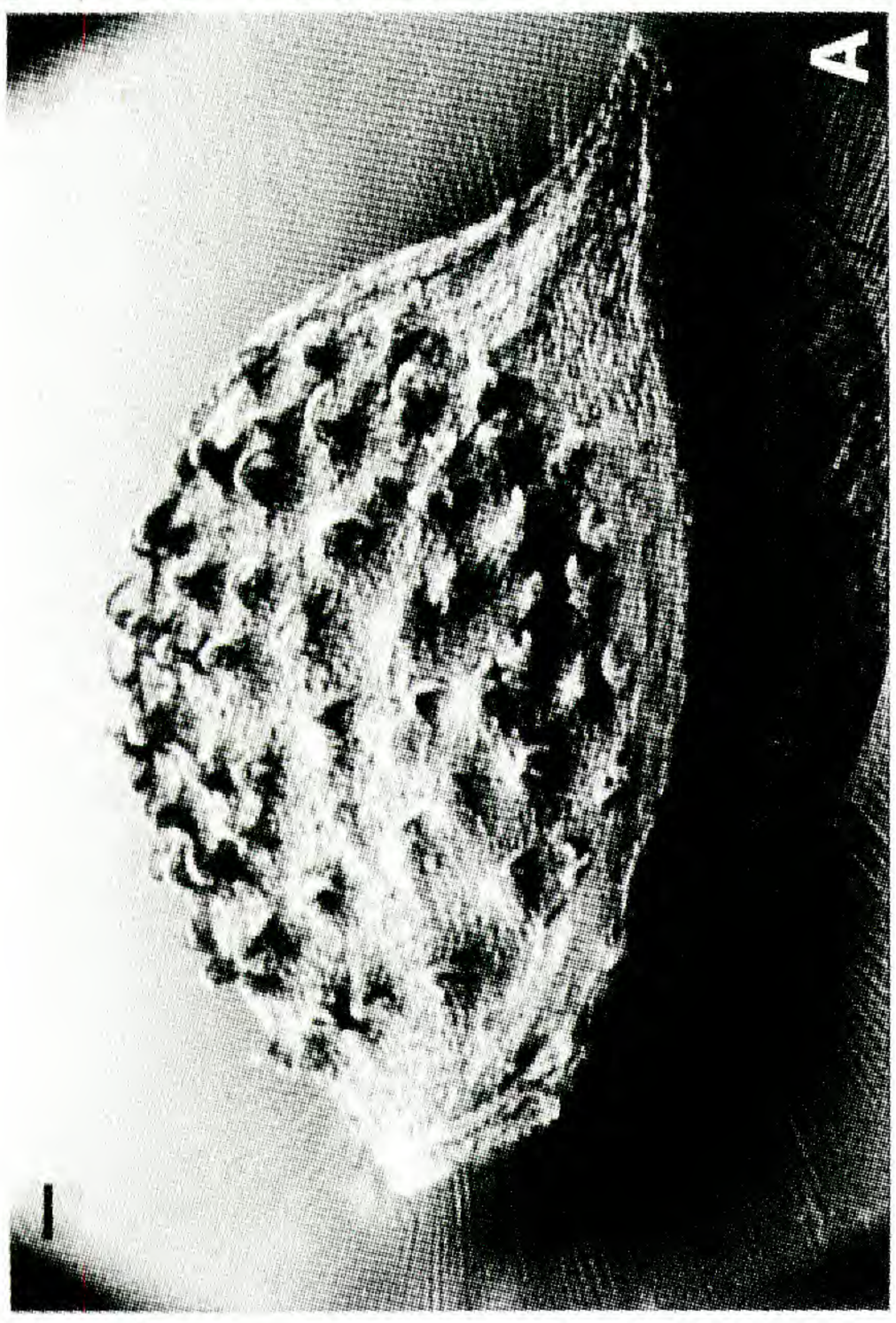
Fig. 4C, D. *R. arvensis*. Spines multicellular, conelike, sometimes recurved, of varying lengths up to 0.57 mm long centrally, 0.85 mm long marginally, present (sometimes absent - Fig. 4D) on both the achene face and the marginal ridge; low ridges often present on the achene face, the surface (including the spines) rough with striations, the margins usually smoother.

TAXONOMIC CLASSIFICATION

RANUNCULUS L. subgenus *Ranunculus* section *Echinella* DC., Prodr. 1:41. 1824. TYPE: *Ranunculus arvensis* L., Sp. Pl. 555. 1753.

Erect to reclining glabrous to variously pubescent annuals with stems 1 – 6 dm tall, simple to freely branching above. Leaves basal and cauline or chiefly cauline, the basal simple and variously lobed and parted to pinnately compound, typically 2 – 8 cm wide; petioles 1 – 21 cm long. Cauline leaves alternate, generally similar to basal leaves, upwardly reduced, usually petiolate. Inflorescence 1(– 2)-flowered, axillary or opposite the leaves, sessile or pedunculate, the peduncles lengthening to 5 cm in fruit. Sepals 3 or 5, spreading to reflexed, usually deciduous, 1 – 7 mm long, variously pubescent; petals 3 or 5, yellow, narrowly elliptic to obovate, 1 – 10 mm long, the nectary scale truncate, entire. Achenes 4 – 60, orbicular to subrotund, compressed to rounded, the





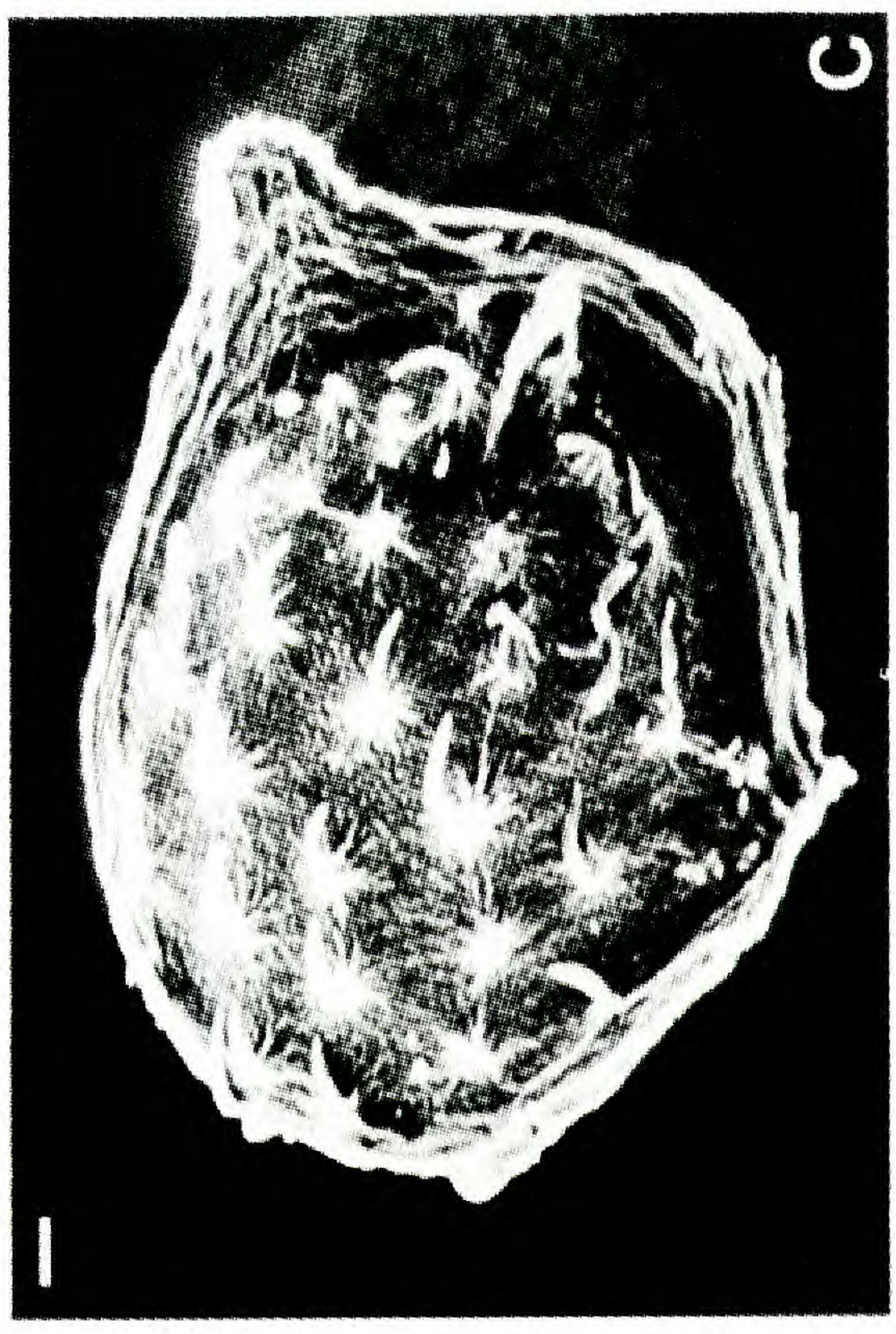
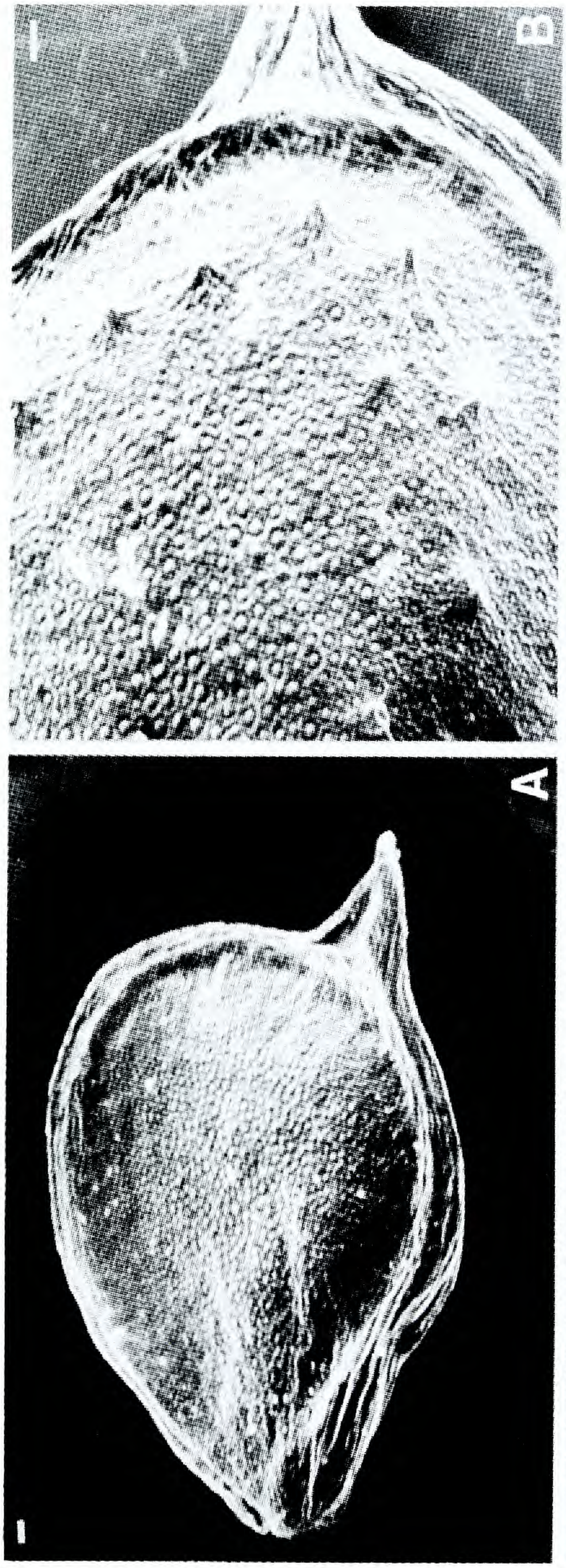


Figure 1. Scanning electron micrographs of achene surfaces. Scale = 100 μm. A, B: *Ranunculus parviflorus*. C,D: *R. platensis*.



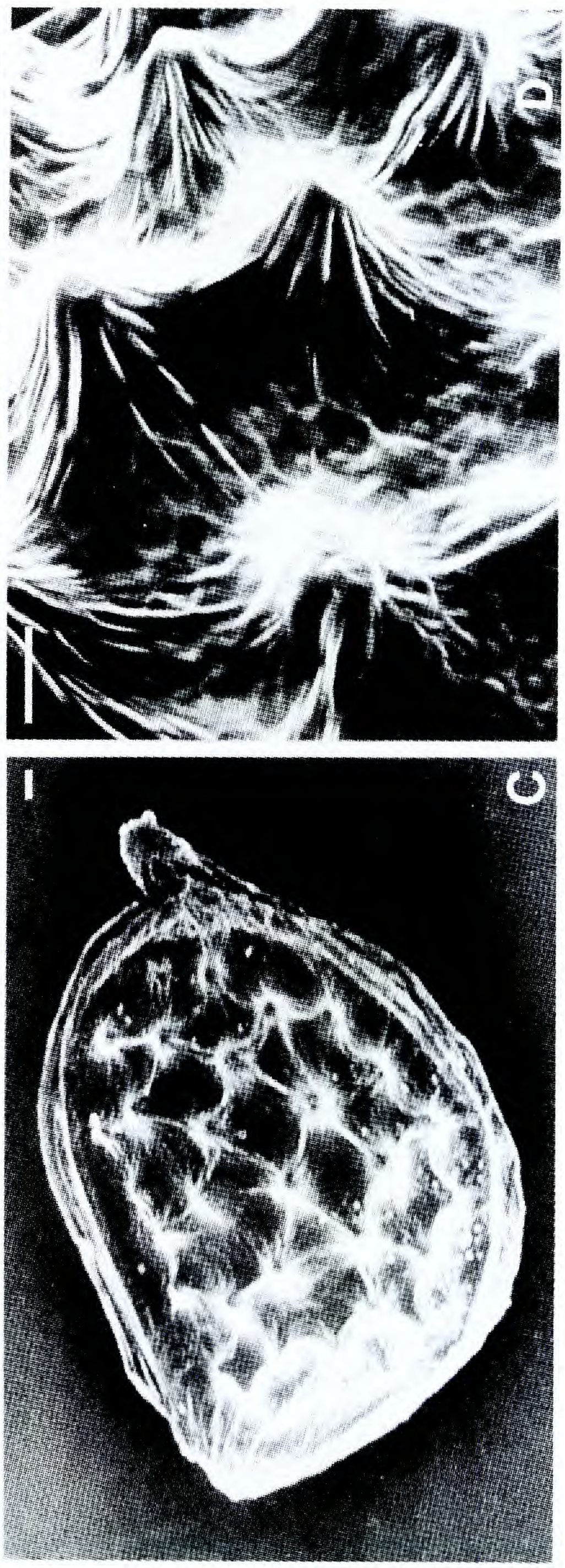
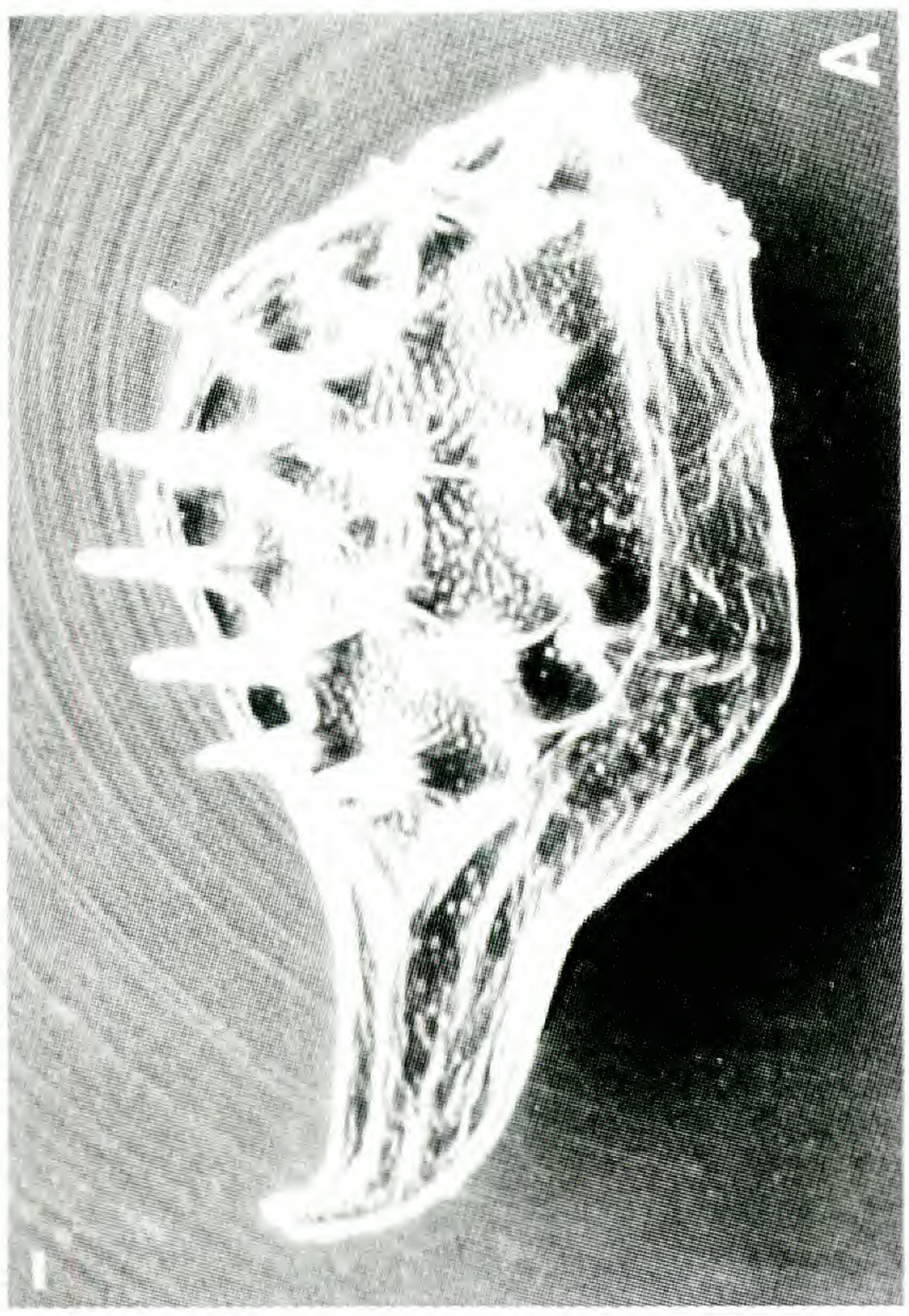


Figure 2. Scanning electron micrographs of achene surfaces. Scale = 100 μm. A, B: *Ranunculus sardous*. C, D.: *R. trilobus*.



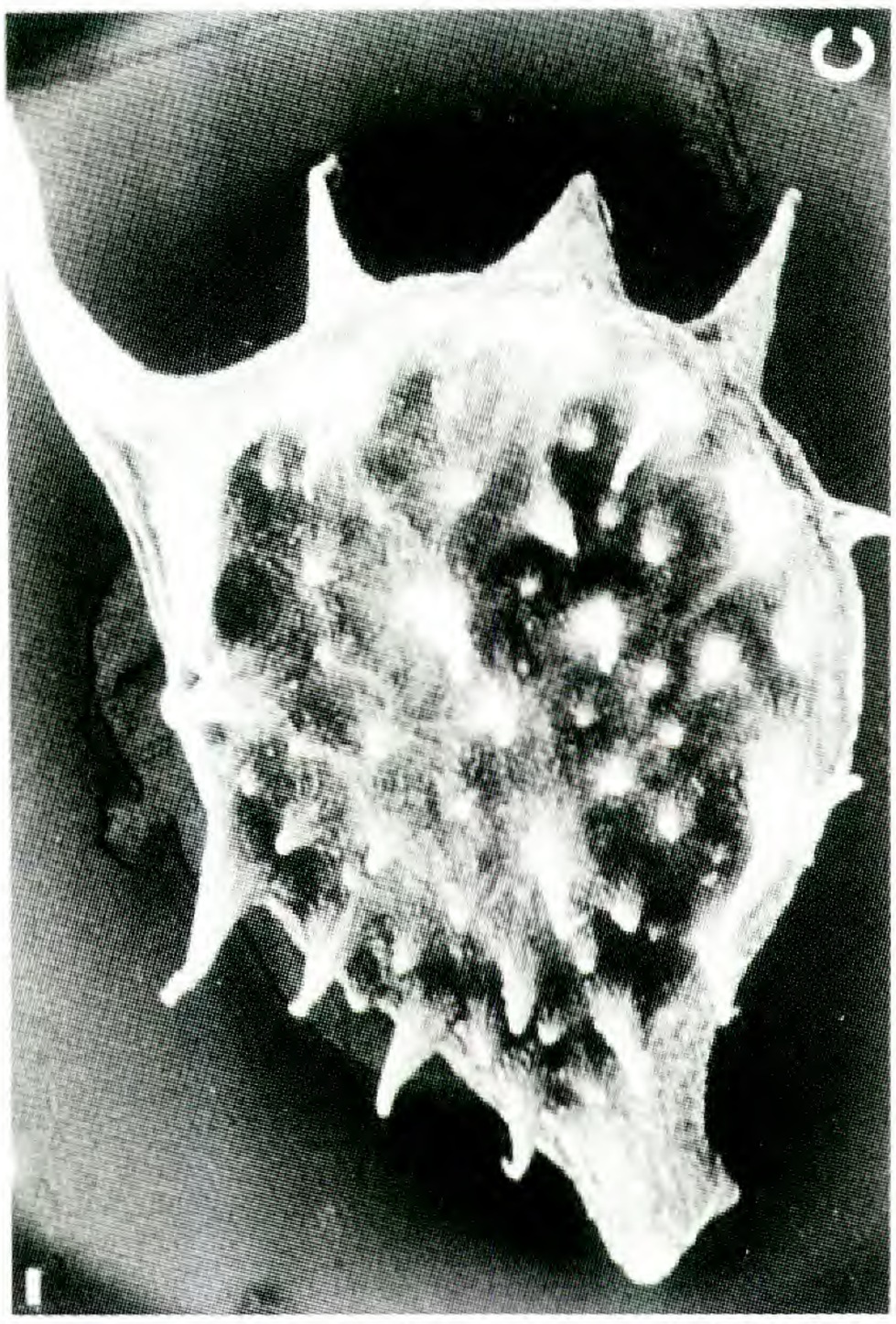


Figure 3A, B. Scanning electron micrographs of achene surfaces of *Ranunculus marginatus*. Scale = 100 μm.

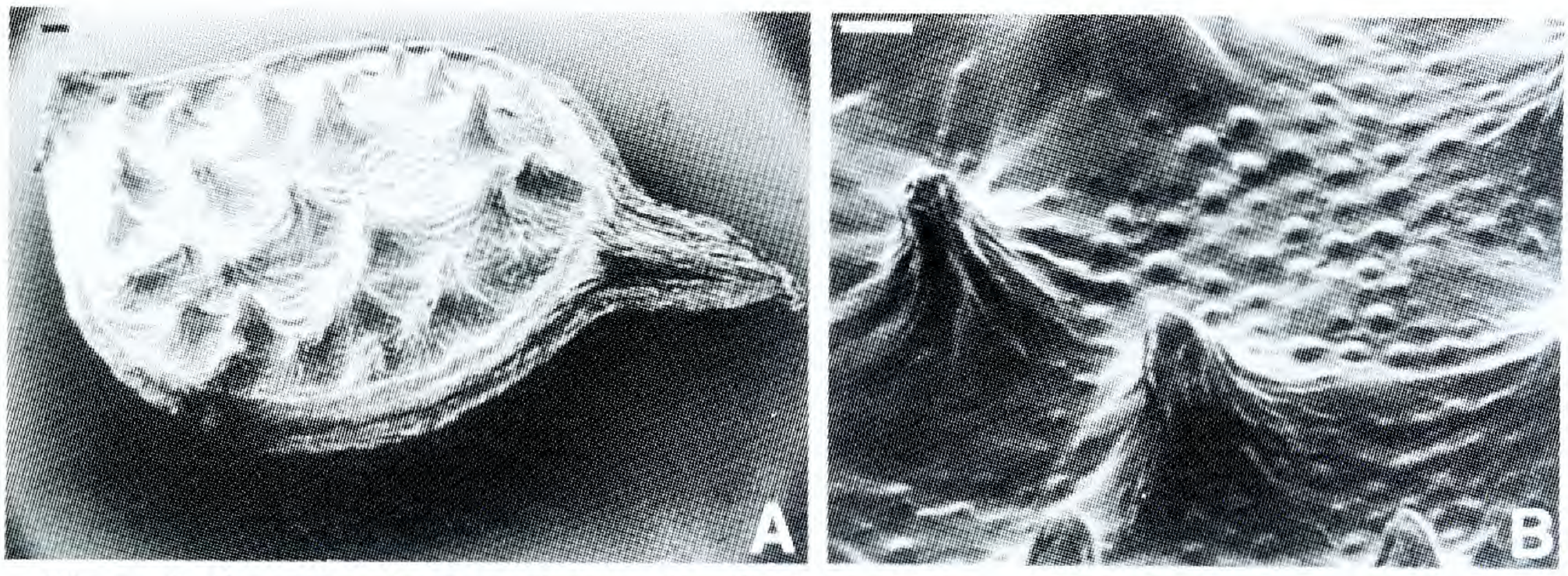


Figure 4. Scanning electron micrographs of achene surfaces. Scale = 100 μm. A, B: *Ranunculus muricatus*. C, D: *R. arvensis*.

bodies 2–5 mm long, discs variously sculptured with recurved trichomes or with short protuberances to stout spines, the margins smooth to spiny; beaks minute to 3 mm long, straight to curved or hooked. Fruiting receptacles globose to ellipsoid or pyriform, 1–5 mm long, generally pubescent. Chromosome numbers: $n = 8$, 14, 16, 24. Adventive from South America (*R. platensis*) or Europe and established in lawns, moist fields, roadside banks and ditches, and waste places.

KEY TO SPECIES OF RANUNCULUS SECT. ECHINELLA WITHIN THE SOUTHEASTERN UNITED STATES

1. Flowers pedunculate, the peduncles usually elongating in fruit, axillary; sepals and petals usually 5; achenes with recurved trichomes or with short protuberances to stout spines ..... 2.
1. Flowers sessile, opposite the petioles; sepals and petals 3; achenes with recurved trichomes only ..... 1. *R. platensis*
   2. Petals 1–3 mm long; mature achenes with multicellular projections, each bearing a short recurved trichome; receptacles glabrous ..... 2. *R. parviflorus*
   2. Petals 3 mm or more long; mature achenes short protuberant (rarely smooth) or with straight to curved spines of varying lengths; receptacles pubescent (see Table 2) ..... 3.
      3. Achenes short protuberant (or sometimes more or less smooth) to short spiny, the bodies less than 3 mm long; achene beaks usually less than 0.5 mm long ..... 4.
      3. Achenes conspicuously spiny, the bodies usually more than 3 mm long; achene beaks at least (0.75) 1 mm long ..... 5.
         4. Achene discs sparsely protuberant to smooth; petals more than 5 mm long; plants more or less hirsute ..... 3. *R. sardous*
         4. Achene discs with numerous short spines; petals less than 5 mm long; plants with a few scattered villous hairs ..... 4. *R. trilobus*
            5. Achenes 9 or fewer, in a single whorl; achene discs and margins with spines of varying lengths; largest leaves compound, the ultimate segments linear to obovate ..... 5. *R. arvensis*

5. Achenes usually 10 or more, not in a single whorl; achene discs tuberculate to long-spiny, the margins smooth; largest leaves simple, broadly cordate to suborbicular and more or less 3 − 5-parted, the segments crenately lobed or toothed . . . . . 6.
   6. Achene discs usually stout-spiny, the spines ca 0.5 mm long; achene beaks at least 1.5 mm long; peduncles usually shorter than the subtending leaf; plants often subglabrate . . . . . 6. *R. muricatus*
   6. Achene discs short-spiny, the spines usually less than 0.2 mm long; achene beaks ca 1 mm long; peduncles usually longer than the subtending leaf; plants sparsely hispid . . . . . 7. *R. marginatus*

1. R. PLATENSIS Sprengel, Syst. Veg. 5:586. 1827. Weak-stemmed pilose annual; stems 2 − 4 dm long. Leaves mostly cauline, alternate, 3-parted, reniform, 1.5 − 2.0 cm wide, segments 3 − 5-lobed; upper leaves gradually reduced; petioles 2 − 5 cm long. Inflorescence 1(− 2)-flowered; flowers solitary (or 2), sessile, scattered along the stem opposite the leaves. Sepals 3, concave, 2 mm long; petals 3, ca 2 mm long. Achenes subrotund, 1.2 mm broad, with short multicellular projections, each projection bearing a slender recurved trichome, margins narrow; beaks relatively broad, curved, minute. Fruiting receptacles globose, 1 mm long, glabrous or pilose. Spring. Sandy clearings along streams, moist fields, and road sides, etc., rare, but locally abundant, especiallly in SE La; cp. Ala, Fla, Ga, La, Miss, and NC. [Tex]. Similar to *R. parviflorus* (No. 2).

2. R. PARVIFLORUS L., Syst. Nat. Ed. 10:1087. 1759. Erect to lax, hirsute to softly pilose, slender annual; stems 1 − 4 dm tall, freely branching. Basal leaves shallowly to deeply 3 − 5-parted, reniform to cordate-rotund, 2 − 5 cm wide, lobes or segments crenate to sharply toothed; petioles 3 − 10 cm long. Cauline leaves alternate, similar to basal leaves, upwardly reduced, short-petiolate. Inflorescence 1-flowered, axillary; peduncles 1 − 4 mm long, lengthening to 20 mm in fruit. Sepals 5, spreading, soon deciduous, narrowly ovate, ca 1 mm long, densely pubescent; petals 5, yellow, narrowly elliptic, 1 − 3 mm long. Achenes subrotund, 1 − 2 mm broad, discs brownish-protuberant, protuberances terminating in a short recurved trichome, margins conspicuous, greenish, nearly smooth; beaks deltoid, hooked, ca 0.5 mm long. Fruiting receptacles globose, 1 − 1.3 mm long, glabrous. ($n = 14$) Spring, summer. Fields and waste places; chiefly cp. and pied. SE except Del and WVa. [Tex, Okla, and Mo].

3. R. SARDOUS Crantz, Stirp. Austr. Fasc. 2:84. 1763. Erect to suberect usually hirsute annual (perennial?) with the overall habit of *R. bulbosus*; stems 1 − 6 dm tall, usually freely branching. Basal leaves simple, 3-parted to pinnately compound, 2 − 4(10) cm wide; segments widely tri-

TABLE 2. The spiny achene group of *Ranunculus* section *Echinella*.

CHARACTERS	ARVENSIS	MARGINATUS	MURICATUS	SARDOUS	TRILOBUS
Basal leaves	simple, trifid to trilobed or trisected	simple, ± lobed to deeply parted, rarely compound	Simple, ± lobed to deeply parted, rarely compound	mostly compound	(simple) . . . compound
Petal color	yellow	deep yellow	deep yellow	pale yellow	pale to deep yellow
Petal length (mm)	6 – 8	3 – 4	5 – 8	5 – 10	3 – 5
Achene head shape	flattened	flattened-globose	flattened-globose	globose	globose
No. achenes/head	4 – 9	10 – 20	10 – 20	30 – 40	40 – 60
Achene body length (mm)	4 – 5	2 – 3.5	3 – 5	2.5 – 3	3(2)
Achene beak length (mm)	2.5 – 3	(0.75) – 1	1.5 – 2.5	0.5	0.5
Achene face	spiny	spiny	spiny	protuberant to smooth	spiny
Achene margins	spiny	smooth	smooth	smooth	smooth
Maximum protuberance or spine length (mm)	facial: 0.57 marginal: 0.85	0.17	0.60	0.05	0.16
Fruiting receptacle length (mm)	1 – 2	2	2	2	3 – 5

angular-obovate, variously lobed and incised; petioles 3 – 21 cm long. Cauline leaves alternate, generally similar to basal leaves, petiolate. Inflorescence 1-flowered, axillary; peduncles 3 – 5 cm long. Sepals 5, reflexed, deciduous, ovate, 3 – 5 mm long, pilose; petals 5, yellow, narrowly elliptic, 5 – 10 mm long; stamens 25 – 50. Achenes discoid, 2 – 3 mm long and broad, discs sparsely protuberant to smooth, glabrous, margins conspicuously rimmed; beaks deltoid, 0.2 – 0.5(1) mm long, hooked to straight. Fruiting receptacles pyriform, 2 mm long, pubescent. ($n = 8$, 24) Spring, summer. Low wet fields and waste places; chiefly cp. and pied. Ala, Ark, Ga, Ky, La, Miss, NC, SC, Tenn, and Va. [Tex, Okla, Mo, Ill, Pa, and NJ]. *R. parvulus* L.—Small (1933). Frequently *R. sardous* is confused with *R. bulbosus* L., and therefore to aid in determining specimens referable to these two species a supplemental key is provided.

Plants soft-based annuals; petals 5 – 8(10) mm long; achenes smooth to protuberant, more or less uniformly thick throughout or slightly bulged in the center, the faces generally orbicular, usually flat ..... *R. sardosus*

Plants cormose perennials; petals 8 – 14 mm long; achenes smooth, unevenly thick, the apex much thicker than the base, the faces asymmetrically obovate to orbicular, variously bulged ..... *R. bulbosus*

4. R. TRILOBUS Desf., Fl. Atlant. 1:437. 1798. Sparsely pubescent annual similar to but overall generally larger than *R. sardous*. Basal leaves simple and 3-foliolate, the largest 3 – 7 cm wide. Petals 5, 3 – 5 mm long; stamens 10 – 20. Achenes 40 – 60, 2 – 3 mm long, the discs with numerous short spines; beaks short deltoid, 0.2 – 0.5 mm long. Fruiting receptacles ellipsoid, 3 – 5 mm long, pubescent. ($n = 16$) Spring. Low clearings, fields, and wet roadside ditches, locally common; cp. Ala, Fla, La, and SC. [Tex]. Apparently recently introduced from southwestern Europe. This species can be confused with *R. marginatus* (No. 7) and to facilitate determining specimens, a supplemental key is added.

Achene heads globose, achenes tightly packed, 40 – 60 per head; achene beaks 0.5 mm or less long; fruiting receptacles 3 – 5 mm long ..... *R. trilobus*

Achene heads globose to flattened; achenes usually spreading, ca 20 per head; achene beaks 0.75 – 1 mm long; fruiting receptacles ca 2 mm long ... *R. marginatus*

5. R. ARVENSIS L., Sp. Pl. 555. 1753. Erect, glabrous to sparsely hirsute annual; stems 1.5 – 5 dm tall, simple to freely branching above. Basal leaves simple, cuneate-obovate, ca 1 cm wide, trifid to trilobed or trisect; petioles 1 – 5 cm long. Cauline leaves alternate, compound, dissected into linear, entire or narrowly cuneate-oblanceolate incised or lobed segments to 5 mm wide; petiolate or sessile. Inflorescence 1-flowered, axillary; peduncles 1 – 3.5 cm, lengthening to 5 cm in fruit. Sepals 5, spreading, deciduous, narrowly elliptic, 4 – 7 mm long, hirsute; petals 5, yellow,

obovate, 6 – 8 mm long. Achenes 4 – 9, obliquely obovoid, compressed, 4 – 5 mm long (excluding the beak) and 3 – 4 mm broad, discs and margins diversely sculptured, typically with spines of varying lengths; beaks stout, subulate, straight to curved, 2.5 – 3 mm long. Fruiting receptacles subglobose, 1 – 2 mm long, pubescent. ($n = 16$) Spring, summer. Fields and waste ground, uncommon; chiefly cp. and pied. Ark, Ga, Miss, NC, SC and Tenn. [Mo, Ohio, and NJ]. Including *R. arvensis* var. *tuberculatus* (DC.) Koch, a form with merely tuberculate (short spiny) achenes.

6. R. MURICATUS L., Sp. Pl. 555. 1753. Reclining or weakly erect glabrous to sparsely hirsute annual (perennial?); stems 0.5 – 5 dm tall, freely branching. Basal leaves shallowly to deeply 3 – 5-parted or rarely pinnately divided, broadly cordate or reniform to subrotund, 2 – 8 cm wide, the segments lobed or crenate to sharply toothed; petioles 4 – 15 cm long. Cauline leaves alternate, similar to the basal leaves, upwardly reduced. Inflorescence 1-flowered, axillary; peduncles usually shorter than the subtending leaf. Sepals 5, spreading to reflexed, deciduous, ovate, 4 – 7 mm long, sparsely hairy; petals 5, yellow, obovate, 5 – 8 mm long. Achenes 10 – 20, obovoid, compressed, 3 – 5 mm long (excluding the beak) and 3 – 3.5 mm broad; discs brownish, usually stout spiny, the spines ca 0.5 mm long, margins conspicuous, greenish, smooth; beaks stout, falcate, 1.5 – 2.5 mm long. Fruiting receptacles subglobose, 2 mm long, pubescent. ($n = 24$) Spring. Low meadows, ditches, and stream banks; cp., rarely inland. Ala, Ark, Fla, La, Miss, and SC. [Tex].

7. R. MARGINATUS D'Urville, Mém. Soc. Linn. Paris 1:318. 1822. Pubescent annual similar to *R. muricatus*. Upper cauline leaves divided into narrowly oblong or linear segments. Peduncles usually longer than the subtending leaf. Petals 5, usually less than 4 mm long. Achenes ca 20, obovoid-orbicular, compressed, ca 3 mm long (excluding the beak), short spiny, the spines usually less than 0.2 mm long; margins smooth, beaks erect, triangular, ca 1 mm long. Fruiting receptacles subglobose, 2 mm long, sparsely pubescent. Spring. Roadside ditches, locally common; cp. Ala and La. [Tex]. In var. *marginatus* the achene discs are smooth, but our plants have spiny achenes and may be distinguished as var. *trachycarpus* (Fischer & Meyer) Azn. See note under *R. trilobus* (No. 4).

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SCHIZAEACEAE IN FLORIDA

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Several status changes have occurred for the Florida members of the Schizaeaceae. The following account brings that information together along with keys and updated distributional information on each taxon. This article is intended to subject that information to public critique prior to its inclusion in the pteridophyte treatment for the Flora of Florida. I openly solicit comments, suggestions, and additional information on these taxa.

KEY TO THE FLORIDA GENERA

1. Fronds vine-like, twining, of indeterminate growth; secondary pinnae arising in pairs from short stalks on the rachis . . . . . *Lygodium*
1. Fronds not vine-like and twining; secondary pinnae not arising in pairs from short stalks on the rachis, or absent 2
   2. Sterile fronds simple, linear and appearing grasslike; lamina essentially wanting or present as mere wings; sporangia borne on distal, linear, apparently digitate segments . . . . . *Actinostachys*
   2. Sterile fronds compound, not appearing grasslike; lamina obviously present; sporangia borne on distinctly pinnately divided segments . . . . . *Anemia*

ACTINOSTACHYS PENNULA (Swartz) Hooker

The species was first discovered in Florida in 1903, by A.A. Eaton (1906) in Dade County, and again found sometime after 1914 at Royal Palm Hammock in Dade County (Small 1938), in Pinellas County in 1952 (Beckner 1953), and in Palm Beach County in 1972 (Alexander 1974). The species is apparently extirpated from the Dade and Pinellas county locations, but is extant in Palm Beach County. *Actinostachys pennula* is widely distributed and common in continental tropical America from Costa Rica to Uruguay and less common to rare, but widespread in the Caribbean. Previous authors on the ferns of Florida have reported the species as very rare, or at least inconspicuous and overlooked; the latter is more likely. Recent searches at the Palm Beach County location have turned up numerous plants (R. Moyroud pers. comm.). Notably, the plants were entirely restricted to rotting *Persea* stumps and logs.

The form of this species known for Florida as well as the Lesser Antilles and Central America formerly went under the name *Actinostachys germanii*

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Fée or *Schizaea germanii* (Fée) Prantl. The "*A. germanii*" form had been distinguished from the more common continental South American *A. pennula* by its smaller stature and the presence of what authors have described as "hairy tubers." These "tubers" have recently been shown to be gametophytes (Wagner & Guevedo 1985). Morphological differences between the two taxa are apparently due to the neotenic nature of the "*A. germanii*" form. The neotenic form is widespread throughout the range of the species and generally occurs in shaded pockets of humus or rotting wood at low elevations. The robust form differs in the habitat types in which it occurs; that of sandy savannas and dry rock outcrops, presumably conditions unfavorable to persistence of the gametophyte. The robust form is not usually found along with its gametophyte. It is still uncertain why the robust form has not been found in Florida.

KEY TO THE FLORIDA SPECIES OF ANEMIA SWARTZ

1. Fronds partially dimorphic with a basal pair of fertile pinnae, mostly more than 1 dm tall ..... *A. adiantifolia*
1. Fronds completely dimorphic, mostly less than 1 dm tall ..... *A. wrightii*

ANEMIA ADIANTIFOLIA (L.) Swartz

The species was first collected in Florida by J.L. Blodgett in 1838 in Monroe County (Small 1938). It occurs in the four southernmost counties and extends northward on the east coast to Palm Beach and Martin counties where it is rare. The species is disjunct to Levy, Citrus, and Sumter counties. Its distribution outside of Florida ranges from the West Indies to Mexico and south through Central America to northern South America.

The distribution of *A. adiantifolia* in Florida appears limited by both the availablility of limestone substrates and cold intolerance. The plants occur in pinelands, hammocks, or other habitats with rocky limestone substrates and exhibit a high (perhaps 100%) occurrence on exposed limestone. The absence of *A. adiantifolia* in apparently suitable limestone habitats farther northward in the state is probably due to its cold intolerance. Several other tropical species of "limestone-loving" ferns are disjunct to the Levy-Citrus-Sumter county area (notably several species of *Asplenium*). The reason for these disjunct populations is still enigmatic, representing perhaps either refugial remnants of former more widespread distributions or anomolous local ecological conditions. Regardless of the reason for these disjunctions, it is noteworthy that *A. adiantifolia* has not spread to neighboring areas with apparently suitable substrate conditions. This further suggests that cold intolerance is a limiting factor in the species' distribution in Florida.

ANEMIA WRIGHTII Baker

Anemia wrightii was first found in Florida by C.V. Delchamps and G. Avery in Dade County near Homestead (Delchamps 1977). Outside of Florida it occurs in Cuba and the Bahamas. Throughout its range the species occurs on moist edges and walls of bare limestone ("pinnacle rock") in open habitats.

Lellinger (1985) reported the plants to be under threat from "expanding agricultural lands." The original Homestead population is adjacent to an airport where this threat is real. However, the species is now known from a second site within the protective confines of the Everglades National Park. The discovery of this second site and its location within the park suggests that the species may not only persist in Florida, but may possibly spread to other areas.

KEY TO THE FLORIDA SPECIES OF LYGODIUM SWARTZ

1. Members of the lateral pairs of pinnules generally 1-pinnate with each primary division a mostly undivided, triangular to lanceolate-oblong segment, generally without basal lobes, if present the lobes are rounded, auriculate and do not point toward the apex; ultimate segments appearing to be articulate, leaving a wiry petiolule after falling off; lamina tissue glabrous abaxially ..... *L. microphyllum*

1. Members of the lateral pairs of pinnules generally more than 1-pinnate, with each primary division a pinnately to subpalmately divided segment, or if undivided, with distinct basal lobes directed at an angle toward the apex; ultimate segments not apparently articulate to their petiolules; lamina tissue sparsely to moderately pubescent abaxially ..... *L. japonicum*

LYGODIUM JAPONICUM (Thunb.) Swartz

Lygodium japonicum is widespread in northern and north central peninsular Florida from Escambia to Duval counties and south to Highlands County. Outside of Florida the species ranges from the Carolinas and Georgia west to Alabama, Mississippi, Louisiana, and Texas. A native of Japan, *L. japonicum* is commonly naturalized, and occurs in wet woods, marshes, roadside ditches, riverbanks, and other wet disturbed sites in circumneutral (*fide* Wherry 1964) soil. The species may be locally abundant. Where naturalized in the greatest numbers, it appears to be following natural river systems in its spread, notably the Suwannee and Apalachicola rivers.

Lygodium japonicum was first collected in Florida in 1932 by Kurtz and E.T. Wherry (Small 1938), but is also known from a 1932 Diddell collection. The Diddell collection (*Diddell s.n.* FLAS!) reported the species as escaped in vacant lots in Miami, but the plants were probably only

persistent from cultivation (cf. Beckner 1968; Nauman & Austin 1978). The species has also been collected in Collier and Broward counties. The Collier County collection (*Scull s.n.* 1935, FLAS!) was of a plant in cultivation and the Broward County collection (*Burch s.n.*, 1986, FAU!) was of a plant only recently escaped. No naturalized populations are known south of Highlands County. To my knowledge, this species is restricted to temperate/warm temperate regions. Intolerance to warm temperatures may explain its absence in the more distinctly tropical and subtropical portions of the state.

LYGODIUM MICROPHYLLUM (Cav.) R. Brown

A native of southeast Asia, *L. microphyllum* is recently naturalized in the United States and is continuing to spread. The earliest collection record of *L. microphyllum* for Florida is 1958; the species seems to have been introduced in the 1940's or 50's (Nauman & Austin 1978). By 1968 it was known from three isolated colonies in Martin and Palm Beach counties (Beckner 1968) and by 1978 it had spread throughout those two counties (Nauman & Austin 1978). It is now known from Broward, Collier, Highlands, Martin, Palm Beach, and Polk counties, Florida. Unlike *L. japonicum*, this species is primarily tropical in its distribution outside of Florida and whether it will remain restricted to tropical portions of the state is uncertain.

Lygodium microphyllum occurs on riverbanks, swamps (especially Cypress swamps), cabbage palm hammocks, and other wet disturbed sites. The species may be very locally abundant, climb to 9 m heights in nearby trees, and form thick mats at the ground level covering considerable areas (Beckner 1968; Nauman & Austin 1978).

Ecological observations on both *L. japonicum* and *L. microphyllum* may prove valuable to population biologists. Both species occur in essentially the same habitat types but, at this writing there are no single sites in which the species have been reported to co-occur. Both, however, are sympatric in Highlands and Polk counties and searches for sites with both species should be directed in those areas. Mixed populations of these species may provide an excellent opportunity to test various theories regarding principles of competitive exclusion with both sporophyte and gametophyte generations.

EXCLUDED SPECIES

ANEMIA CICUTARIA Kunze—A number of herbarium sheets of *A. wrightii* have been misidentified as *A. cicutaria* and the species has been reported to occur in Florida (Correll & Correll 1982; Mickel 1979). The

fact that these two species often co-occur in sympatric portions of their ranges outside of Florida (Correll & Correll 1982) is probably responsible for the error. *Anemia cicutaria* differs from *A. wrightii* in being more densely pubescent, 2 – 3 times rather than 1 – 2 times pinnate, has fertile fronds with several pairs of distinctly petiolulate rather than subsessile pinnae, and ovate to rhombic, broad-based ultimate segments with shallowly crenate rather than lobed margins (Correll & Correll 1982; Mickel 1979). *Anemia cicutaria* may eventually be found in Florida.

LYGODIUM PALMATUM (Bernh.) Swartz—Nearly every author on the Florida fern flora has followed Chapman (1883) in reporting this species for the state. Despite this high number of reports, no populations or specimens exist to document the species' occurrence with the exception of a single collection from Lemon City, Dade County made in 1895 (no collector, FLAS P87!). Wherry (1964) suspected that this specimen represented a cultivated plant, and Correll (1938) seemed to have reservations about accepting the species' occurrence in Dade County. I agree with Wherry (1964) that the specimen probably represents a cultivated plant; suitable habitat is not present in Dade County, nor was it likely to have been present when the Lemon City collection was made. The species' requirements for relatively acid substrates precludes it from many southern Florida habitats that would otherwise seem favorable. Even though locally rare, its wide geographic range and occurrence in the southern Coastal Plain makes Chapman's report of the species seem reasonable, and may be why subsequent authors continued to report the species for Florida. If the species does occur in Florida, it is most likely to be in the panhandle region. Yet, recent studies of that region by Clewell (1985), Wilhelm (1984), and Freeman, et al. (1979) have failed to turn up populations of *L. palmatum*. Additionally, young, sterile, and incompletely unfurled fronds of *L. japonicum* (widespread in northern Florida) superficially resemble *L. palmatum*. The resemblence between these two species makes misdetermination likely, especially if the presence of the Asian *L. japonicum* was unknown to the person identifying the plants. It is unlikely Chapman would have made such a mistake. Chapman's source for the record however, is unknown and he did not cite a specimen. The apparent absence of current populations, herbarium specimens for confirmed former populations, and the possibility of misdetermination have convinced me to exclude the species from the Florida flora.

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THYMELAEA PASSERINA (THYMELAEACEAE) IN OHIO

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ABSTRACT

Thymelaea passerina, a herbaceous weed native to Europe, is reported as new to Ohio. The plant has been previously recorded in North America from Iowa, Kansas, Nebraska, and Illinois. A description of the species and an illustration are included.

The Thymelaeaceae have previously been represented in the Ohio flora by *Dirca palustris* L. (leatherwood), a native shrub, and by *Daphne mezereum* L. (mezereum), a cultivated shrub that occasionally escapes (Braun 1961). A population of *Thymelaea passerina* (L.) Cosson & Germain, a small herbaceous weed from Europe, has been discovered in the state, adding another genus from the family to the flora of Ohio.

The genus *Thymelaea* Tourn. ex Miller consists of woody and herbaceous species found mainly in the northern hemisphere of the Old World, especially in the Mediterranean region. In a recent revision of the genus, Tan (1980) recognized 30 species, two-thirds of which are narrow endemics, and only four of which are considered widespread. Annuals, suffrutescent perennials, and woody species are represented in the genus. Some species appear to be beetle-pollinated. In *T. passerina*, a hermaphroditic, non-apomictic species, seed set is high but pollinators are unknown (Tan 1980).

Thymelaea is represented in North America only by *T. passerina* (Fig. 1). Tan (1980) speculated that it was introduced to North America among seeds of fodder plants. It has been reported from Harrison, Monona, Plymouth, Pottawattamie and Woodbury counties in Iowa, Cloud County in Kansas, Cedar, Merrick and Morrill counties in Nebraska (McGregor et al. 1986; Pohl 1955), and from Kane and Lake counties in Illinois (Mohlenbrock 1982; Mohlenbrock & Ladd 1978; Swink & Wilhelm 1979), where it occurs on railroad embankments and eroded slopes and in pastures. More recently, it has been collected in DuPage County, Illinois

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(Swink, pers. comm.). The Ohio population (several hundred plants) was found in Montgomery County (Butler Twp. sect. 23, near Vandalia) by Stanley J. Stine, Jr. (*Stine 11*, 30 Jul 1985), on a gravelly hillside of eroded Milton silt loam, 700 feet east of National Road (U.S. Rt. 40), west of Cassel Road, in the Taylorsville Reserve, Dayton-Montgomery County Park District, an area which was once a farm, but which has been a reserve for over 50 years. Associated species include *Cornus drummondi* Meyer, *Danthonia spicata* (L.) Beauv., *Erigeron strigosus* Muhl., *Eupatorium altissimum* L., *Juniperus virginiana* L., *Panicum lanuginosum* Ell., *Solidago graminifolia* (L.) Salisb., and *Vitis riparia* Michx. No speculations can be made concerning the origin or date of introduction of the population. A voucher, unidentified, was donated to the Willard Sherman Turrell Herbarium of Miami University (MU), with a duplicate specimen deposited at Kent State University (KE).

Thymelaea passerina was not included in any North American plant identification manual prior to Swink & Wilhelm (1979) and Mohlenbrock (1982). On the basis of these two reports, this species is included in the Kartesz & Kartesz (1980) and Shelter & Skog (1978) checklists. The National List of Scientific Plant Names (Soil Conservation Service 1982) ascribes the plant only to the list's region "5" (Nebraska, Kansas, eastern Colorado), thus not accounting for the Iowa and Illinois reports.

A description of the species (after Mohlenbrock [1982] and Tan [1980], in part) follows:

THYMELAEA PASSERINA (L.) Cosson & Germain

Erect annual from fibrous roots, stem slender, yellow-green, simple or sparingly branched, (10−)15−60 cm tall, glabrous or slightly pilose at the tips. Leaves alternate, subsessile, narrowly lanceolate to linear, 5−20 × 1−2.5 mm, acute, entire, glabrous or with a few hairs on the lower surface, leathery. Flowers perfect, axillary, solitary or clustered, subtending bracts 2, lanceolate, 2−3 mm, ciliate at base. Sepals 4, perianth 2.5−3 mm, appressed pubescent, yellowish, lobes ovate, shorter than the hypanthium, obtuse. Petals absent. Stamens 8. Ovary elongate, hirsute at apex; style short, terminal; stigma capitate. Fruit a 1-locular, 1-seeded capsule enclosed in the persistent hypanthium. Seed brown to black, ovoid, 2−3 mm long. $2n = 18$ (Tan 1980). Flowering late April to August.

Distribution: Widespread in central and southern Europe, eastern, central, and southwestern Asia, and central Russia. Introduced to Australia and North America. No records from South America or southern Africa (Tan 1980).

Figure 1. *Thymelaea passerina*. Left, plant; Center, younger branch before loss of some leaves; Right, persistent hypanthium with enclosed fruit.

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THE RE-INSTATEMENT OF *BORRERIA TERMINALIS* SMALL (RUBIACEAE)

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ABSTRACT

Populations of *Borreria terminalis* Small and *B. verticillata* (L.) G.F.W. Meyer in southern Florida were studied to determine whether the recent reduction of the former to the synonymy of the latter was justified. Vegetative characters were found to distinguish populations but provided no means of separating the species. Marked differences were found between the species in several characters related to flower size. The consistency of the floral differences and the absence of hybrids supported the continued recognition of *B. terminalis* as a distinct species endemic to southern Florida.

John Blodgett collected specimens of a *Borreria* on Big Pine Key, Monroe Co., Florida in the middle part of the 19th century which Chapman (1860) referred to *B. podocephala* DC. var. *pumila* Chapman. This treatment at first was accepted by Small (1913), but he later described the plant as a new species, *B. terminalis* Small (1924). Small differentiated *B. terminalis* from the closely related *B. verticillata* on the basis of flower size. *Borreria terminalis* was listed as endemic to southern Florida in Small's Manual of the Vascular Flora of the Southeastern United States (1933) while *B. verticillata* was not listed as occurring in the area at all. Plants referred to *B. verticillata* were first recorded in southern Florida as a weed introduced into Dade County during the late 1960's. Wunderlin (1979), reviewing *Borreria* (as *Spermacoce*) in Florida, relegated *B. terminalis* to the synonymy of *B. verticillata* without elaboration. Quite apparent differences between the populations referred to *B. terminalis* and *B. verticillata* in Dade County however, indicated the need for further study.

For the last several decades, the name *B. terminalis* Small has been applied to a plant which grows in sites ranging from dry pineland to prairies with a short hydroperiod throughout southern Florida. This plant is most abundant and grows most luxuriantly in areas which are flooded for short periods (1 to 2 months) yearly. The weedy plants referred to *B. verticillata* are clearly a recent introduction to southern Florida. Their distribution is generally sympatric with that of *B. terminalis* in Florida, but they show a preference for drier sites. They grow primarily along road shoulders and in disturbed fields which rarely if ever are flooded.

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Road shoulder populations of this plant are often found adjacent to populations of *B. terminalis*. Other populations of plants in this complex are found in Palm Beach and Martin counties, isolated from the two population groups previously mentioned, growing along road shoulders in wet areas. This population was treated as an element of *B. terminalis* by Long and Lakela (1971).

Collections were made from several populations of plants belonging to this complex in southern Florida (Figure 1). Total flower length (ovary plus corolla), ovary length, ovary width, and width of the corolla limb were measured on fresh flowers. Figure 2 shows flowers from the two species and illustrates how measurments were made. Leaf length and width, ovary length and width, length of corolla tube, and seed length (along the long axis) were measured on dried specimens collected during this study or examined in the herbaria of Everglades National Park (ENP) and Fairchild Tropical Garden (FTG).

Three distinct morphological types were recognized among the collected plants. **Group A**, which represents *B. terminalis* as traditionally recognized, is characterized by linear to lanceolate-linear leaves, little-branched habit, and large flowers. The corolla limb of plants belonging to this type is 2.5 mm or more wide. **Group B**, representing the newly introduced weed, is characterized by relatively broad, elliptic leaves, much-branched habit, and small flowers. The corolla limb on plants of this type is 1.4 – 2.0 mm wide. Plants of **Group C**, from Palm Beach and Martin counties, have long, linear leaves of **Group A** plants and the small flowers of **Group B** plants. All of the groups are identical with respect to seed length (Figure 3).

The populations sampled during this study fall into two groups when ovary length and corolla limb width are considered (Figure 4), even though a large amount of variation is found in both ovary length and corolla limb width within each population. Most of this intrapopulational variation is due to the progressive reduction in size of flowers developed towards the distal end of the inflorescence branches. Plants of **Group A** are clearly separated from plants of **B** and **C**, while the latter two are totally mixed together. It is possible to separate **Group A** from **B** and **C** on the basis of corolla limb width alone (Figure 5) with considerable accuracy. Differences in corolla size are evident on dried specimens, and are very useful in distinguishing plants of **Group A** from plants of **Group C**.

Group B is sharply distinguished from the sympatric **Group A** in leaf shape (Figure 6) as well as flower size. These plants have been growing in close proximity for at least two decades, but no evidence of crossing between any populations has been found. This, and the magnitude of the

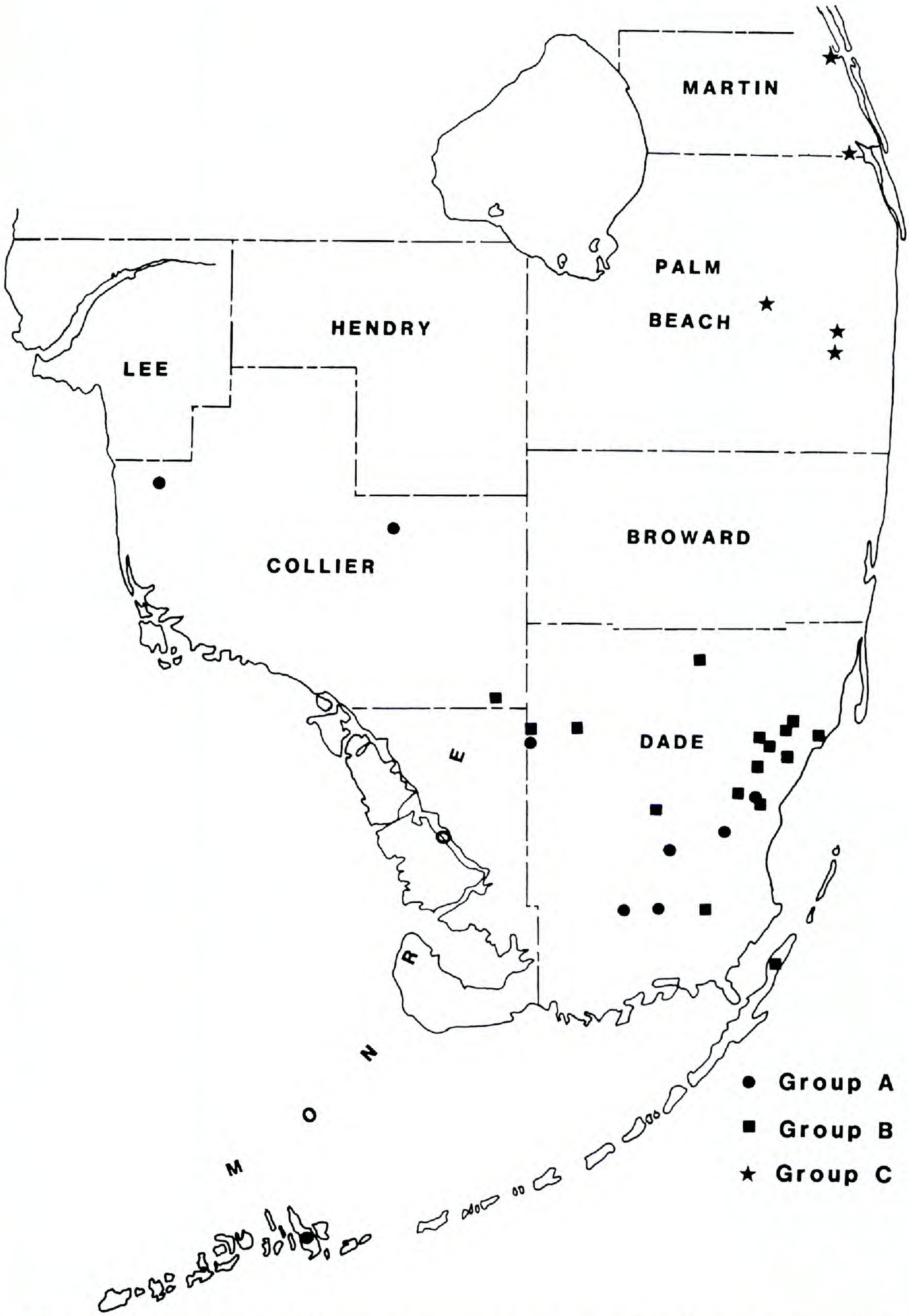

Figure 1. Collection localities of specimens examined during this study. Differences between groups are detailed in the text.

difference in flower size, supports the recognition of two groups as distinct species. Small did not designate a type specimen in his original description of *B. terminalis*, but F.R. Fosberg at the United States National Herbarium has graciously examined early collections of *Borreria* from southern Florida and confirmed that Small's concept of the species was based on the large-flowered plants of **Group A** (pers. comm.).

Plants of **Group C** are not sufficiently distinct from plants of **Group B** to warrant taxonomic recognition. The two groups appear to represent different elements of the widespread and troublesome *B. verticillata-capitata* complex. Plants in **Group B** are identical to plants called *B. verticillata* by Correll & Correll (1982), but as Fosberg (pers. comm.) points out, *B. verticillata* has not been typified, so the correct application of this name is still in doubt.

In addition to differences in overall flower size, *B. terminalis* has larger anthers and larger pollen grains when compared to the other populations. These differences are correlated with flower size and may be due to the reported polyploidy of *B. terminalis* ($2n = 84$, Lewis 1962), a triploid relative to *B. verticillata* ($2n = 28$, Miege 1962; Lewis et al. 1966).

Using the name *B. vericillata* for the small-flowered plants of **Groups B** and **C** (with the reservations noted above), we may delineate the species as follows:

Corolla tube 1.25 – 2.5 mm long; ovaries of larger flowers over 1.5 mm long, 1.0 mm wide; leaves linear, 2 – 5 cm long, 0.15 – 0.4 cm wide ..... *B. terminalis*

Corolla tube 0.6 – 1.0 mm long; ovaries of larger flowers usually under 1.5 mm long, 0.7 mm wide; leaves linear to elliptic, 1 – 5 cm long, 0.2 – 0.8 cm wide ..... *"B. verticillata"*

Borreria terminalis Small, Bull. Torrey Bot. Club 51:387. 1924.

Borreria podocephala DC. var. *pumila* Chapman, Fl. Southern U.S. 175. 1860.

Specimens examined (**Group A**):

FLORIDA. **Collier Co.**: roadside, Alligator Alley, 30 May 1979, *Black & Black 384* (ENP, FTG); in dry scattered-pine savanna along Route 839, E of Jerome, 12 May 1981, *Correll 51768* (FTG). **Dade Co.**: open pineland in pitted limestone, W of Old Cutler Road, just S of Cutler Hammock and canal, 15 Sept 1973, *Correll & Correll 40047* (FTG); in periodically wet area in open pineland near fire tower on road running SW of road to Anhinga Trail, Everglades National Park, 29 Dec 1973, *Correll & Long 40970* (FTG); park entrance, Everglades National Park, 19 Dec 1955, *Craighead s.n.* (ENP); burned-over pineland, Seminole Wayside Park, 21 Nov 1972, *Gillis 11504* (FTG); rocky pineland with red soil, SW 272 St-152 Ave, 22 Feb 1983, *Herndon 682* (FTG); low, rocky pineland, near gate 4, Block F, Long Pine Key, Everglades National Park, 26 Feb 1983, *Herndon 686* (FLAS, FTG); rocky pineland with sandy soil, SW 115 Ave-163 St, 6 Mar 1983, *Herndon 697* (FTG); short saw grass prairie off Context Road, approx. 2.5 km W of L31, 12 Mar 1983, *Herndon 699* (FTG, US); pinelands at entrance to Everglades National Park, on US

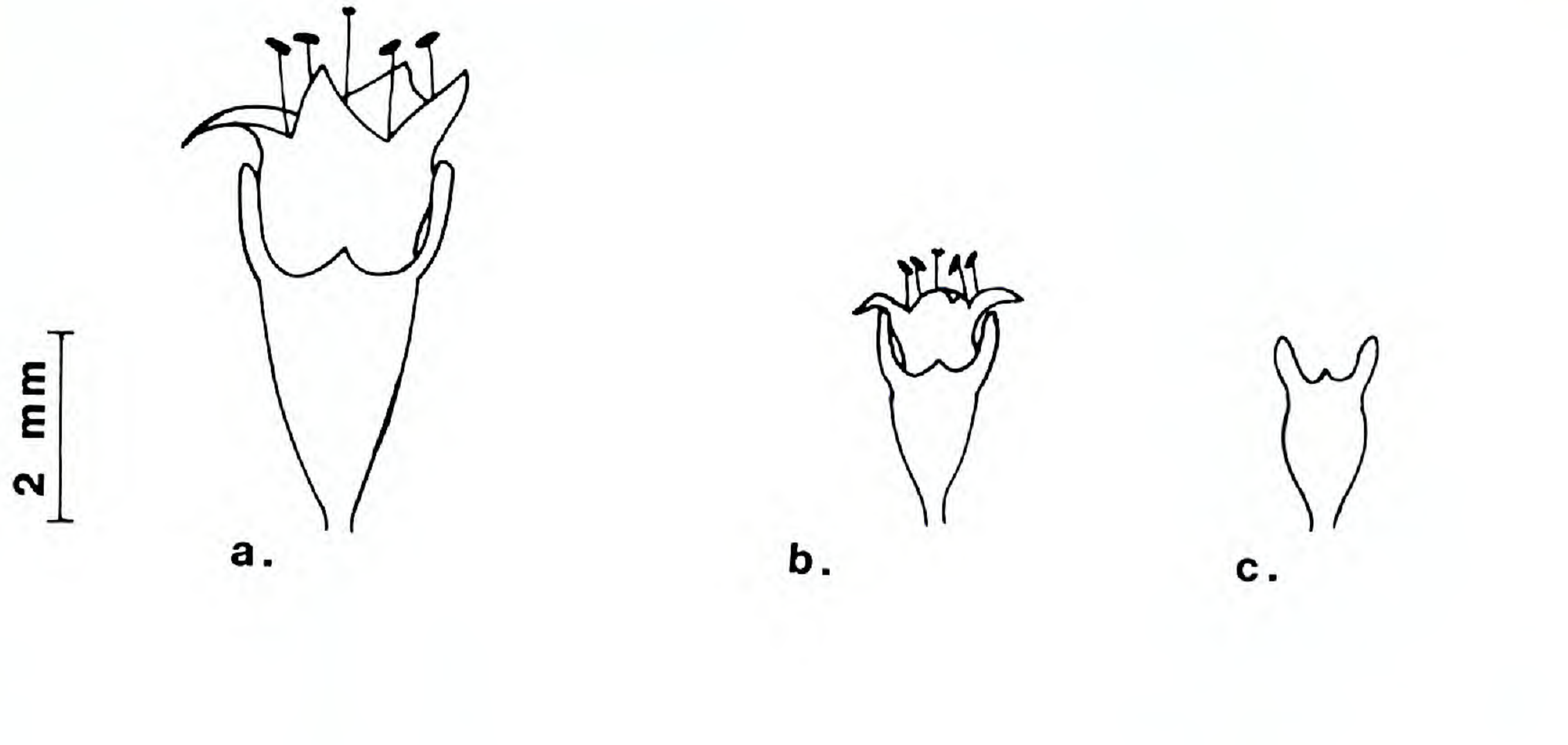

Figure 2. a) Flower of *Borreria terminalis* at anthesis. b) Flower of *B. verticillata* at anthesis. c) Mature fruits of *B. verticillata*. d) Diagram illustrating the measurements taken from fresh flowers.

27, 23 Oct 1983, *Herndon 949* (FLAS, FTG, RSA, US); pinelands just W of Glade 2, Long Pine Key, Everglades National Park, 6 Nov 1983, *Herndon 964* (FLAS, FTG, US); rocky grassland, S side of 216 St., 7.4 mi SW of intersection with 194 Ave, W of Goulds, 12 Mar 1975, *Hill & Popenoe 2570* (FTG); edge of citrus grove just W of Homestead General Aviation Airport, 5 Feb 1978, *Popenoe 1160* (FTG); Long Pine Key, Everglades National Park, 3 Apr 1952, *Robertson s.n.* (ENP); pineland, on new burn, Long Pine Key, Everglades National Park, 17 Apr 1952, *Robertson s.n.* (ENP); high pinelands, Block J, Long Pine Key, Everglades National Park, 11 May 1964, *Sullivan 28* (ENP). **Monroe Co.**: in savanna-like area, Big Pine Key, 8 Feb 1977, *Correll & Popenoe 48080* (FTG).

Grows in pinelands and prairies. Known only from Collier, Dade, and Monroe counties, Florida.

BORRERIA VERTICILLATA (L.) G.F.W. Meyer, Prim. Fl. Esseq. 83. 1818.

Spermacoce verticillata L., Sp. Pl. 102. 1753.

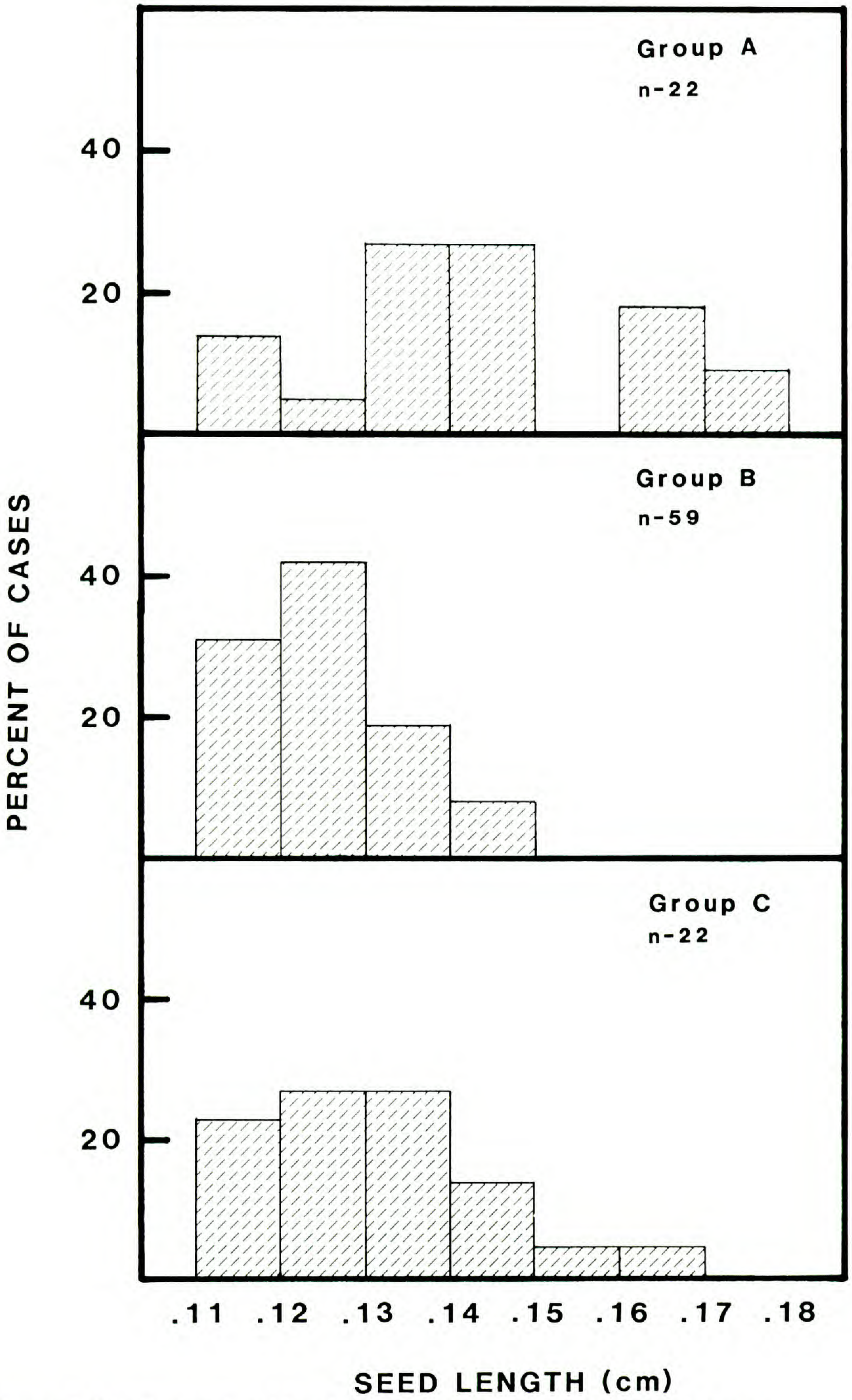

Figure 3. Distribution of seed lengths in the three morphological groups of *Borreria*.

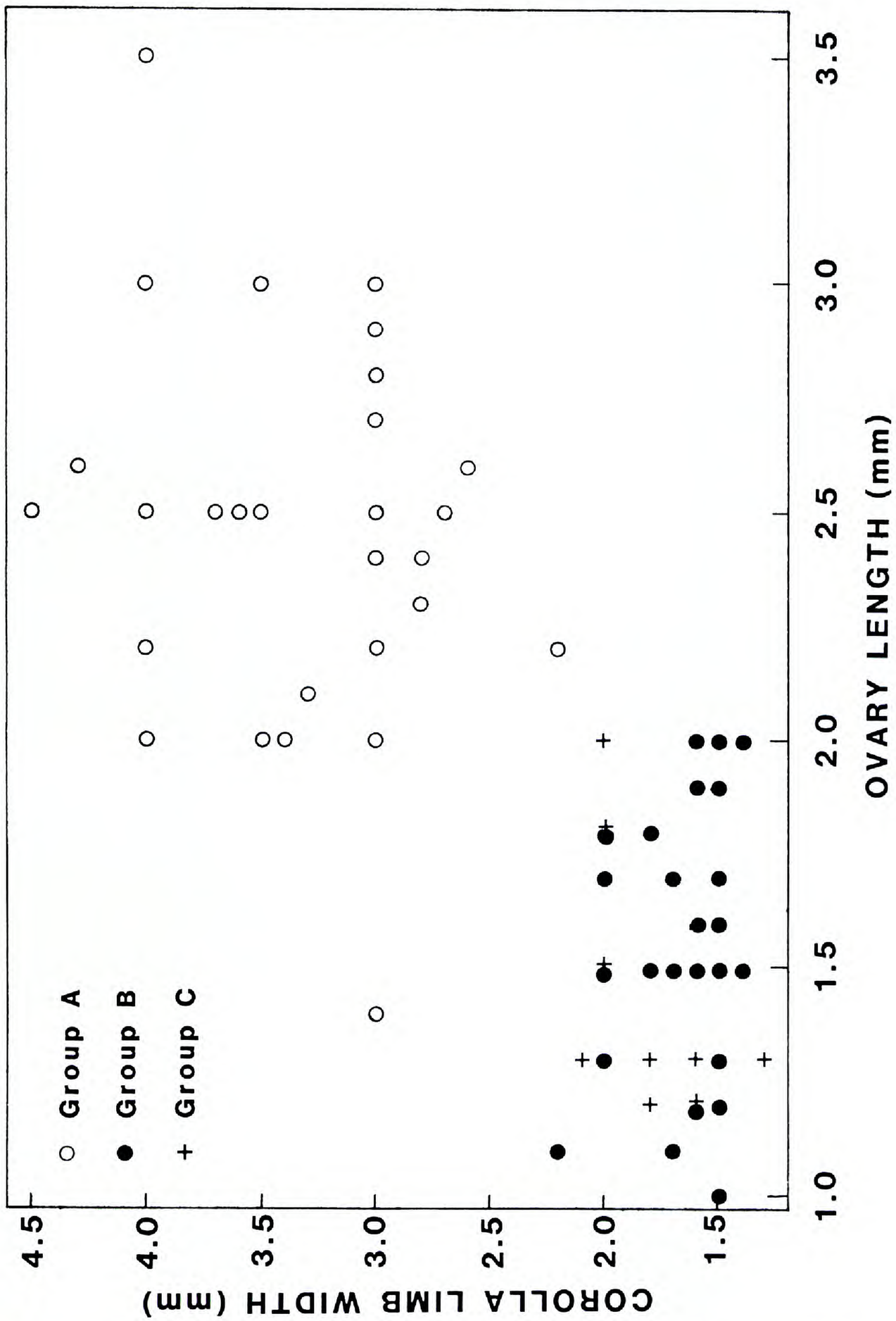

Figure 4. Scatter diagram of corolla disk width and ovary length from fresh flowers in the three morphological groups of *Borreria*.

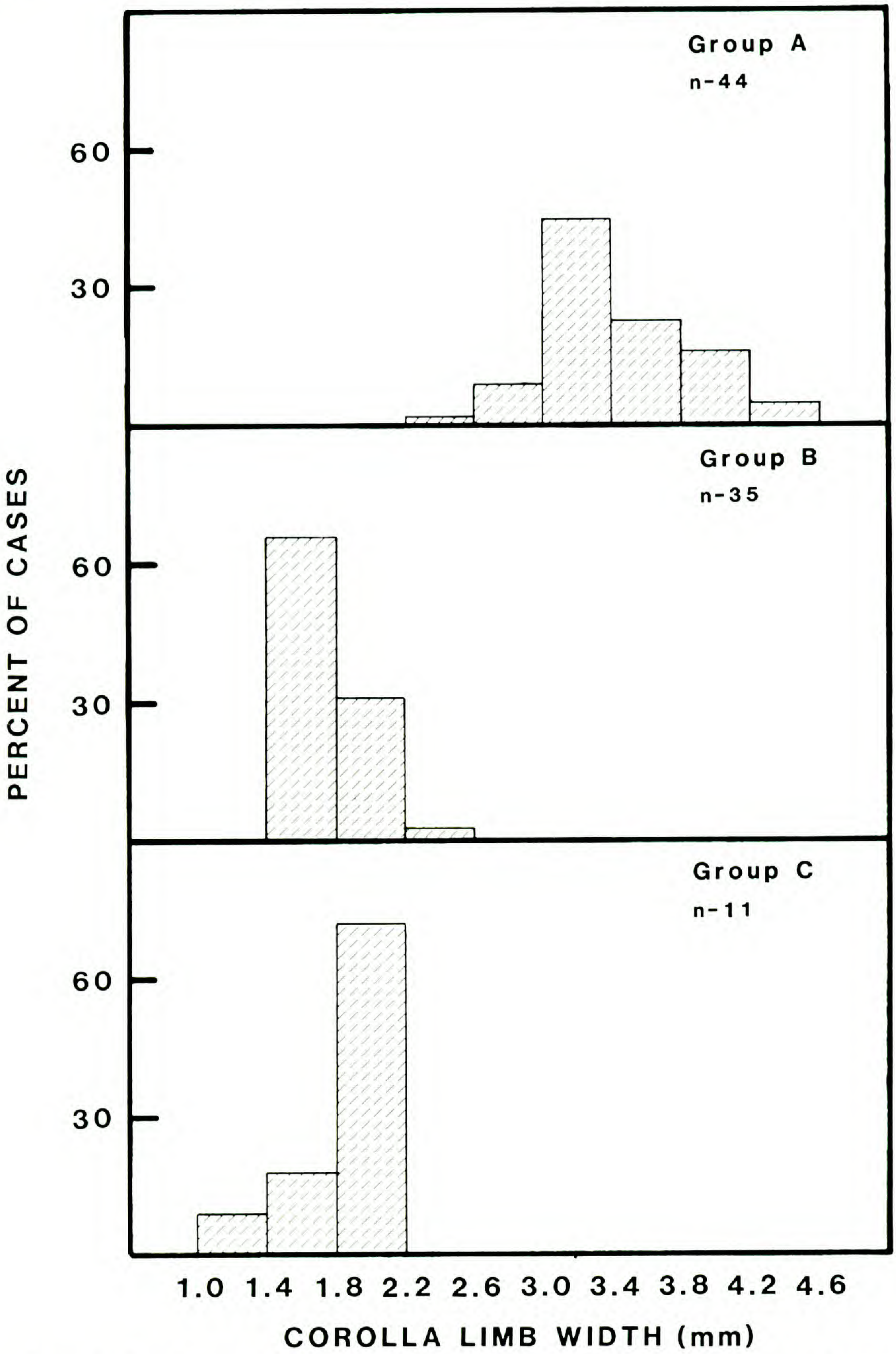

Figure 5. Distribution of corolla limb widths in the three morphological groups of *Borreria* (measurements from fresh flowers).

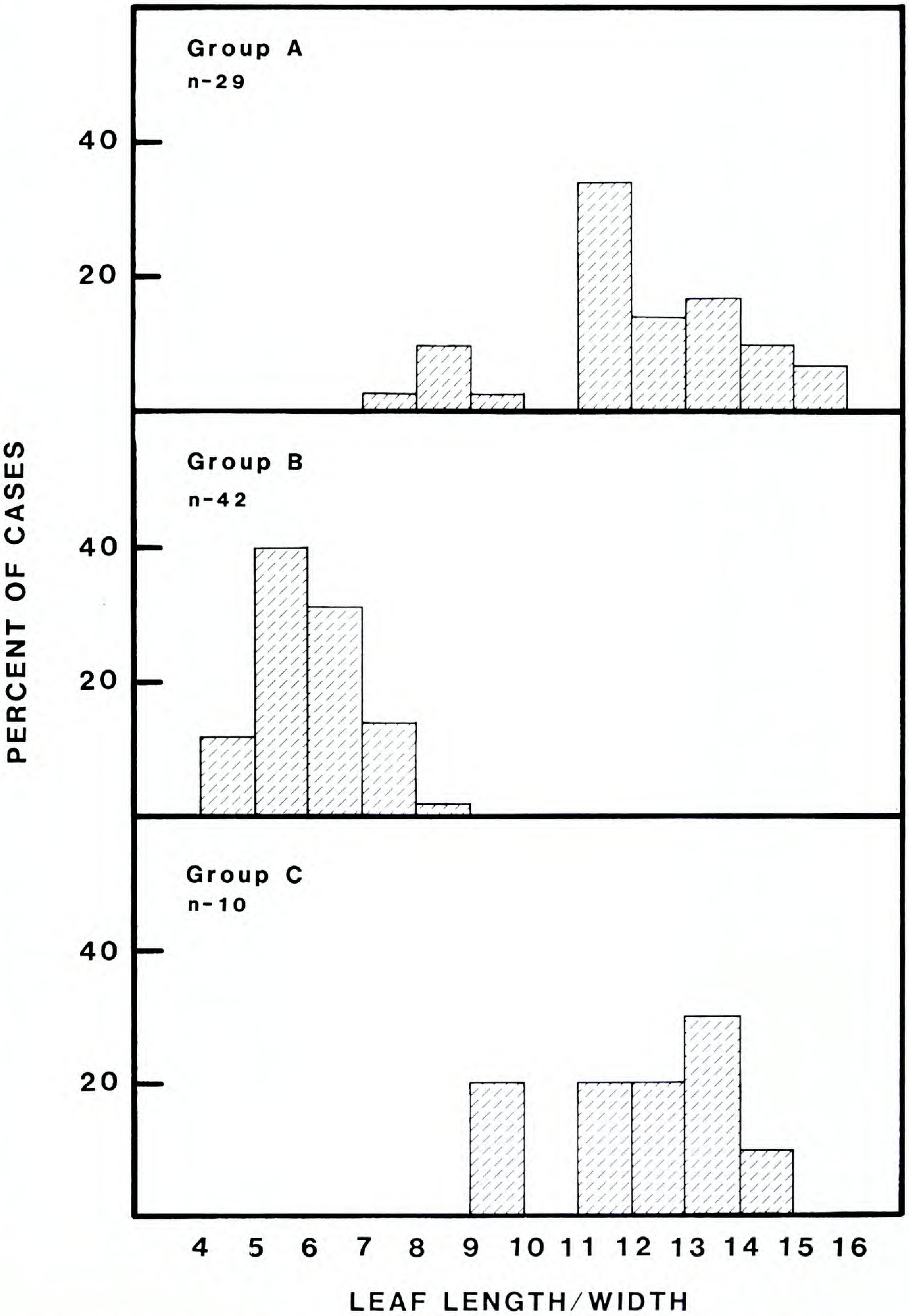

Figure 6. Distribution of the leaf length/width ratios in each of the three morphological groups of *Borreria* (measurements from dried specimens.)

Specimens examined (**Group B**):

FLORIDA. **Collier Co.**: lawn of house, Fifty-mile bend, US 41, 28 Jan 1979, *Herndon 122* (FTG). **Dade Co.**: on filled, vacant land, Red Road and canal S of Miami International Airport, 5 Feb 1969, *Avery 589A* (FTG); South Miami, disturbed soil in railroad right-of-way, SW 62 Ave & US 1, 8 Jul 1974, *Avery 1502* (FTG); weed in lawn, SW 160 St-107 Ave, 4 Mar 1979, *Herndon 173* (FTG); growing in mowed lawn beneath chain-link fence, SW 160 St-108 Ave, 2 Mar 1980, *Herndon 327* (FLAS, FTG, RSA, US); weed in parking area, Miccosukee Restaurant, US 41, 18 mi W of SR 27, 21 Nov 1982, *Herndon 666* (FTG, US); mowed field, Tamiami Campus, Florida International University, 21 Feb 1983, *Herndon 681* (FTG, US); roadside, near Lake Chekika State Recreation Area, 5 Mar 1983, *Herndon 690* (FTG, US); disturbed soil at the edge of a small hammock, Bird Drive Park, SW 40 St-72 Ave, 13 Mar 1983, *Herndon 701* (FLAS, FTG); weed in parking lot, Colonial Drive Elementary School, SW 160 St-109 Ave, 19 Dec 1983, *Herndon 994* (FLAS, FTG, RSA); disturbed road shoulder, SW 117 Ave-88 St, 9 Feb 1984, *Herndon 1021* (FLAS, FTG); disturbed roadside, SW 152 St-137 Ave, 14 Feb 1984, *Herndon 1026* (FTG); mowed lawn around parking lot, SW 12 St-13 Ave, Miami, 2 Apr 1984, *Herndon 1047* (FLAS, FTG); on dry road shoulder, SR 27, 4 mi S of intersection with US 27, 28 May 1984, *Herndon 1073* (FLAS, FTG, US); wayside rest area, intersection SR 41 & 94, 27 Mar 1975, *Hill 2662* (FTG); Miami International Airport, Plant Inspection Station, 27 Nov 1968, *Popenoe s.n.* (FTG). **Monroe Co.**: on dry road shoulder, intersection Card Sound Road and SR 905, Key Largo, 6 May 1984, *Herndon 1058* (FTG, US).

Introduced into Dade County, Florida ca 1967. Rapidly spreading at the present time with populations known along road shoulders from northern Key Largo in Monroe Co. through Highlands Co., Florida.

Specimens examined (**Group C**):

FLORIDA. **Martin Co.**: 4 May 1962, *Lakela s.n.* (FTG); flat open pineland, grassy, with *Sabal palmetto, Serenoa repens, Befaria* & *Lyonia*, N of Port Salerno, off US A1A, 4 May 1962, *Lakela 25033* (ENP, FTG); dry area near Pinegrove Campground, Johnathan Dickenson State Park, 17 May 1975, *Popenoe 358* (FTG). **Palm Beach Co.**: in open pineland along Indiantown Road, SR 706, about 1 mi E of Jupiter exit on turnpike, 7 Feb 1975, *Correll & Popenoe 44271* (FTG); growing on road shoulder, Donald Ross Rd, approx. 1 km E of SR 811, 28 Jul 1984, *Herndon 1091* (FLAS, FTG, US); growing on road shoulder, Hood Road approx. 3 km W of SR 811, 28 Jul 1984, *Herndon 1092* (FTG); growing on road shoulder, PGA Blvd at Loxahatchee Slough, 28 Jul 1984, *Herndon 1093* (FTG, US).

Apparently first found by O. Lakela ca 1962. Status as a native questionable. Known from Martin and Palm Beach counties in Florida.

ACKNOWLEDGMENTS

Roger Sanders (FTG), Richard P. Wunderlin (USF), and F. Raymond Fosberg (US) reviewed earlier versions of the manuscript. In addition, Dr. Fosberg graciously examined early collections of *Borreria terminalis* to determine the correct application of the name. I am indebted to the curators of the herbaria at Fairchild Tropical Garden and Everglades National Park for allowing use of their collections.

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NOTES ON *CYNANCHUM* (ASCLEPIADACEAE)

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ABSTRACT

Preparation of a treatment of *Cynanchum* for the Chihuahuan Desert Flora resulted in a reevaluation of the varieties of *Cynanchum barbigerum* (Scheele) Shinners and recognition of a new variety of *C. maccartii* Shinners.

CYNANCHUM BARBIGERUM—In his treatment of Texas Asclepiadaceae other than *Asclepias*, Shinners (1964) recognized two varieties of *Cynanchum barbigerum*, distinguishing them in his key and discussion only on the basis of flower size. His *C. barbigerum* var. *barbigerum* was distinguished as having corollas 3.6 – 5.2 mm in length and a range from the Edwards Plateau to south Texas and into northeastern México. The new variety *C. barbigerum* var. *breviflorum* Shinners had shorter corollas, 2.8 – 3.2 mm long, and occurred largely in trans-Pecos Texas south into Chihuahua, México. His studies implied that the two taxa differed only in flower size and if that were the case they certainly could be justifiably recognized as allopatric varieties. The two taxa were accepted and similarly treated in Correll and Johnston (1970). However, my analysis of these taxa reveals that in addition to corolla length differences, the taxa also show consistent differences in 1) stem vestiture; 2) the point or origin of corona horns on the column; 3) the total length of corona horns; and 4) the amount of the corona horn's exsertion beyond the anthers. In my opinion the two taxa clearly can be recognized as distinct species separated by characters given in the following key:

A. Stem internodes with decurved hairs 0.1 – 0.2(–0.3) mm long in one line; corollas 2.8 – 3.2 mm long; corona horns 1.3 – 1.8 mm long, exserted above anthers 0.8 – 1 mm, often incurled at tips, adnate to the gynostegium ..... 1. *C. pringlei*

AA. Stem internodes glabrous; corollas (3.2 –)3.6 – 5.5 mm long; corona horns 1.0 – 1.3 mm long, exserted above anthers 0.2 – 0.3 mm, seldom incurled at tips, adnate to gynostegium and corolla at base ..... 2. *C. barbigerum*

1. CYNANCHUM **pringlei** (Gray) Henrickson, comb. nov. *Metastelma pringlei* Gray, Proc. Amer. Acad. Arts 21:397. 1886. TYPE: MÉXICO. CHIHUAHUA, 1885, *Pringle 62* (HOLOTYPE: GH!).

SIDA 12(1): 91 – 99. 1987.

Cynanchum barbigerum (Scheele) Shinners var. *breviflorum* Shinners, Sida 1(6):360. 1964. TYPE: TEXAS. Brewster Co.: Big Bend National Park, Chisos Mountains, granite peak in center of Basin, 5500 ft, 19 Jul 1952, *Grady L. Webster 4340* (HOLOTYPE: SMU!).

Twiggy-based, spreading, climbing, often mat-forming, lactiferous vines 0.5 − 1 m tall and in diameter; stem internodes 11 − 35 mm long with decurved hairs 0.1 − 0.2(−0.3) mm long arranged in one line below nodes, and this line alternating on sides of successive internodes, otherwise glabrous. Leaves mostly drooping; petioles 2 − 5(−6) mm long, pubescent adaxially along channel; leaf-blades linear-lanceolate to oblong-lanceolate, oblong-ovate, 11 − 17(−34) mm long, (2 −)3 − 8(− 10) mm wide, acute, apiculate-mucronate at tip, rounded to briefly cordate at base, at margins entire, revolute when dry, green and glabrous with 3 − 5 lateral veins beneath, usually antrorsely puberulent along margins. Inflorescences mostly of solitary umbels of 2 − 6(− 12) flowers borne on peduncles 0 − 2 mm long and pedicels 1.2 − 2.5(−4) mm long, both sparsely puberulent as stems in lines; bracts thin, lanceolate, 0.6 − 1.2 mm long; calyx lobes lance-ovate, lanceolate to slightly ovate, (0.8 −)1 − 1.5 mm long, 0.3 − 0.5 mm wide, acute, glabrous; corollas 2.8 − 3.2(−4) mm long, white, drying yellowish-cream; corolla tubes 0.9 − 1.1 mm long; corolla lobes oblong-lanceolate, 2.0 − 3.1 mm long, 0.7 − 1.2 mm wide, thickened at tip and along margins, glabrous outside, densely white bearded with erect wavy hairs 0.2 − 0.7 mm long near tip and diminishing in size along mid margins, centrally hispid with antrorse hairs 0.3 − 0.5 mm long inside; corona horns subulate to filiform, 1.3 − 1.8 mm long, 0.2 − 0.3 mm wide above base, exserted above anther head for 0.8 − 1 mm, but shorter than corolla, often somewhat incurled or coiled at tip, adnate to gynostegium 0.1 − 0.3 mm below anther head, adnate abaxially

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Fig. 1. *Cynanchum pringlei*, *C. barbigerum*, and *C. maccartii*. a − f. *C. pringlei*. a.—Habit showing narrow, lanceolate leaves and umbellate, interpetiolar inflorescences. b.—Node showing single line of hairs along petiole margins and along internodes. Note paired glands at node. c.—Section of flower with two petals and one corona horn removed showing densely bearded inner petal surfaces, and long, subulate, distally incurved corona horns that strongly overtop anther head. d.—Pollinarium with pollinia ca 0.4 mm long showing broad arms. (a − d. from *Henrickson & Wendt 12082*) e.—Mature follicle with smooth exocarp. f.—Mature seed with coma (e − f. from *Chiang et al., 9015f*). g − i. *C. barbigerum*. g.—Node showing sparse hairs along petiole margins but glabrous internodes. Note glands. (from *Graham & Johnston 4525*). h.—Flower with two petals and one corona horn removed showing strongly bearded inner petal surfaces, shorter corona horns that are basally adnate to petal margins. i.—Pollinarium with larger corpusculum and pollinia ca 0.38 mm long. (h − i. from *Fryxell 3651*). j − o.—*C. maccartii*. j − l.—*C. maccartii* var. *latifolium*. j.—Habit showing broad leaves, interpetiolar inflorescences. k.—Flower with two petals removed showing distinctly shorter hairs on inner petal surfaces and moderately short corona horns. l.—Pollinarium ca 0.25 mm in maximum length, note distinctive differences when compared to figs. d − i. (j − l. all from *Hinton 17935*). m − o. —*C. maccartii* var. *maccartii*. m.—Stem with leaves, inflorescences (*Henrickson 11742*). n.—Flower with two

petals removed. Note smaller size when compared to k. o.—Pollinarium ca 0.25 mm in maximum length. (n – o. from *Johnston et al. 11911*). p.—Bivariate graph showing comparisons of leaf length (ordinate) and leaf width (abcissa) for *C. maccartii* var. *latifolium* (open circles) and *C. maccartii* var. *maccartii* (solid circles). Delineation by Bobbi Angell. Magnifications as indicated; scale in a, holds for j, m; in c, holds for b, g.

to upper corolla tube; gynostegium stipe 0.5 −0.7 mm long; anther appendages ovate, ovate-orbicular, 0.2 − 0.3 mm long and wide, scarious, midveins thickened, anther margins 0.3 − 3.3 mm long. Follicles narrowly fusiform, 4 − 6.2 cm long, 5 mm wide, glabrous, smooth; seeds reddish-brown, 5 − 6 mm long; coma 2 −2.5 cm long, white. (Fig. 1a − f).

On rocky limestone, sandstone hillsides in *Agave* scrub, Izotal, up to oak chaparral in the Chihuahuan Desert Region from trans-Pecos Texas (Brewster, Presidio, Jeff Davis counties) south to eastern Chihuahua, northern Durango, west and central Coahuila and northern Zacatecas (Fig. 2) from 800 − 1800 m elevation, with flowers from July to September. *R.M. Steward 466* (GH, LL) reports the common name of "Corona de la Novia." Throughout its range the species shows some diversity in leaf size, along with corolla and corona horn size. Leaf size appears related to local habitat and the amount of shading. Certain collections along the eastern margin of the Chihuahuan Desert in Nuevo León, México have long corollas to 5.5 mm long (as in *C. barbigerum*) but the corona horns are also very long, measuring to 1.8 mm in length and surpassing the anther heads (as in *C. pringlei*). These plants occur in the range of *C. pringlei* and have hairy stems as in *C. pringlei* leading me to conclude they are just *C. pringlei* with very long corollas. The specimens are from western Nuevo León: *Chiang, Wendt & M.C. Johnston 7964* (LL) from 1.5 km W of El Penuelo, near 24°34′ N lat, 100°47′ W long; *Bennett, Torke, Wieder & Dunn 646* (LL) from 15 mi N of Matahuala; and *Hinton 17660* (TEX) from El Barrial, near Galeana.

2. CYNANCHUM BARBIGERUM (Scheele) Shinners, Field & Lab. 19:65. 1951. *Metastelma barbigerum* Scheele, Linnaea 21:760. 1848 (Jan 1849). TYPE: TEXAS. Comal Co.: cedar woods in rocky soil, New Braunfels, Jun − Aug 1846, *Lindheimer 459* (HOLOTYPE: unknown; ISOTYPES: GH − two sheets!). The location of Scheele types is unknown (Stafleu & Cowan 1985).

Twiggy based, spreading to climbing, mat-forming, lactiferous vines 0.5 − 1 m tall and in diameter; stem internodes 12 − 42 mm long, glabrous. Leaves mostly drooping with sparsely curled-puberulent petioles 1.5 − 4(−8) mm long; leaf-blades lanceolate to oblong-lanceolate, 10 − 30(−54) mm long, 3 − 8(− 15) mm wide, tapering to an acute, apiculate tip, rounded to slightly cordate at base, at margins entire, drying revolute, green, closely bullate, glabrous except along sunken midvein above, sometimes sparsely pubescent with upcurved hairs 0.1 − 0.3 mm long above, more gray-yellow green beneath, lateral veins 5 − 6, evident only when leaves are over 4 mm wide. Inflorescences mostly of solitary

umbels of 2 – 6(– 9) flowers borne on peduncles 0.2 – 1.5(– 3) mm long, pedicels 2 – 3 mm long, both glabrous; bracts thin, lanceolate, 0.6 – 1.0 mm long; calyx lobes ovate, oblong-ovate, (0.6 –)0.8 – 1.3 mm long, 0.4 – 0.6 mm wide, acute, scarious margined, glabrous; corollas 3.2 – 5.2 mm long, white, drying yellowish outside; corolla tubes 0.8 – 1 mm long; corolla lobes oblong-lanceolate, (2.2 –)2.8 – 3.6 mm long, 0.8 – 0.9 mm wide at base, strongly bearded inside near tip with dense woolly hairs 0.2 – 0.5 mm long, hispid at mid corolla lobes with stiff, erect to declined, transparent hairs 0.3 – 0.5 mm long; corona horns borne 0.1 – 0.2 mm below anther heads, linear-acicular, 1.0 – 1.3 mm long, 0.1 – 0.2 mm wide, attached to midline of corolla lobe and gynostegial tube at about the same level, extending ca 0.2 – 0.3(– 0.5) mm above anther head; gynostegium stipe 0.5 – 0.6(– 0.7) mm long; anther appendages ovate, ovate-orbicular, 0.2 – 0.3 mm long and wide, scarious, midvein thickened; anther margins 0.3 mm long. Follicles narrowly fusiform, 4.5 – 6.7 cm long, 5 – 6 mm wide, glabrous, smooth, dark brown; seeds reddish-brown, 5 – 6 mm long, coma 2 – 2.5 cm long, white. (Fig. 1g – i).

In clay, caliche, limestone and granite flats, slopes, banks in coastal scrub, Tamaulipan scrub, mesquite thickets, chaparral, and disturbed areas from central and south Texas from Terrell and Val Verde counties east to Llano and Travis counties south along coast from Nueces County south into Nuevo León and Tamaulipas (Fig. 2) from sea level to about 850 m elevation, with flowers from (March) June to September.

Though there is some variation in flower characters the species can be reliably distinguished by its glabrous stems. In addition to the characters given above, minor differences also occur in the shape of the translators and pollinia.

Both species have been described in the genus *Metastelma* on the basis of their umbelliform cymes, and ascending to spreading corolla lobes. *Metastelma* and many other genera were combined into *Cynanchum* L. by Woodson (1941) [see also the discussions in Sundell (1981)].

While recognizing the taxa as distinct species, the relationship of *Cynanchum pringlei* to *C. barbigerum* basically remains the same. Both species tie into a group of species with densely bearded inner corolla surfaces and an earlier version of this paper combined the above species as subspecies of *Cynanchum schlechtendalii* (Dcne.) Standl. & Steyerm. along with *C. trichophyllum* L. Williams, and *C. chiapensis* (Gray) L. Williams as they all seem to form a wide ranging complex extending from Central America into Mexico. It was eventually realized, however, that although the taxa shared certain distinctive characters they each have distinct

character states and are probably best recognized as distinct species. *Cynanchum schlectendalii* has short flowers as in *C. pringlei*, but also has short coronas and long gynostegia, and though somewhat similar to *C. barbigerum*, the latter had much longer corollas. *Cynanchum trichophyllum*, in contrast, has densely vestitured leaves.

CYNANCHUM MACCARTII—Dr. B.L. Turner, during a late-night study of *Cynanchum*, recognized a broad-leaved, geographical race of *C. maccartii* as a distinct variety. *Cynanchum maccartii* is similar to *C. barbigerum* but differs in the very short, thick, matted hairs on the inner surface of the corolla lobes that are only 0.1 – 0.2 mm long as compared to 0.2 – 0.5 mm long for *C. barbigerum*. The broad leaved variety recognized by Turner is described below.

CYNANCHUM MACCARTII Shinners

Twiggy-based, twining-climbing lactiferous vines 0.5 – 2(– 4) m tall; stem internodes 13 – 45 mm long, glabrous or with decurved hairs 0.2 – 0.3 mm long in one line. Leaves mostly drooping; petioles 2 – 5(– 11) mm long, mostly pilose in adaxial channel with curved hairs or glabrous; leaf-blades linear-lanceolate, oblong-lanceolate, oblong-ovate to ovate, 10 – 32(– 50) mm long, 2 – 8(– 17) mm wide, acute to rounded, apiculate at tip, broadly cuneate, rounded to briefly cordate at base, at margins entire, revolute when dry, dark green, finely bullate-granulate, mostly pilose with curved hairs along midvein and along proximal margins or sparsely so throughout above, glabrous, more gray-green, with lateral veins visible beneath. Inflorescences mostly of solitary umbels of 3 – 8 flowers borne on peduncles 0.5 – 1.5 mm long, pedicels 0.2 – 4 mm long, both glabrous, occasionally pilose; bracts thin, lanceolate to deltate, 0.4 – 0.7 mm long, 0.2 – 0.4 mm wide; calyx lobes ovate to lance-ovate, 0.5 – 1.3 mm long, 0.4 – 0.6 mm wide, acute to obtuse, glabrous; corollas 1.8 – 3(– 4) mm long, white to cream-white, tubes 0.5 – 1.5 mm long, corolla lobes oblong-lanceolate, 1.3 – 2.6 mm, 0.6 – 1.0 mm wide, thickish with scarious margins, reflexed-spreading, inner surface uniformly pubescent-canescent with thick hairs to 0.1 mm long, or the distal hairs to 0.2 mm long, with central lower portions obscurely hispid with transparent, deflexed, stiff hairs to 0.1 mm long, glabrous outside; corona horns separate, narrowly deltate to lanceolate, 0.7 – 1.0 mm long, 0.2 – 0.45 mm wide and clasping and decurrent at base, tapering to a narrow attenuate to acuminate tip, surpassing anther head by 0.3 mm, adnate to gynostegium immediately below anther head; gynostegium 0.7 – 1.0 mm long. Follicles narrowly fusiform, 4 – 6 cm

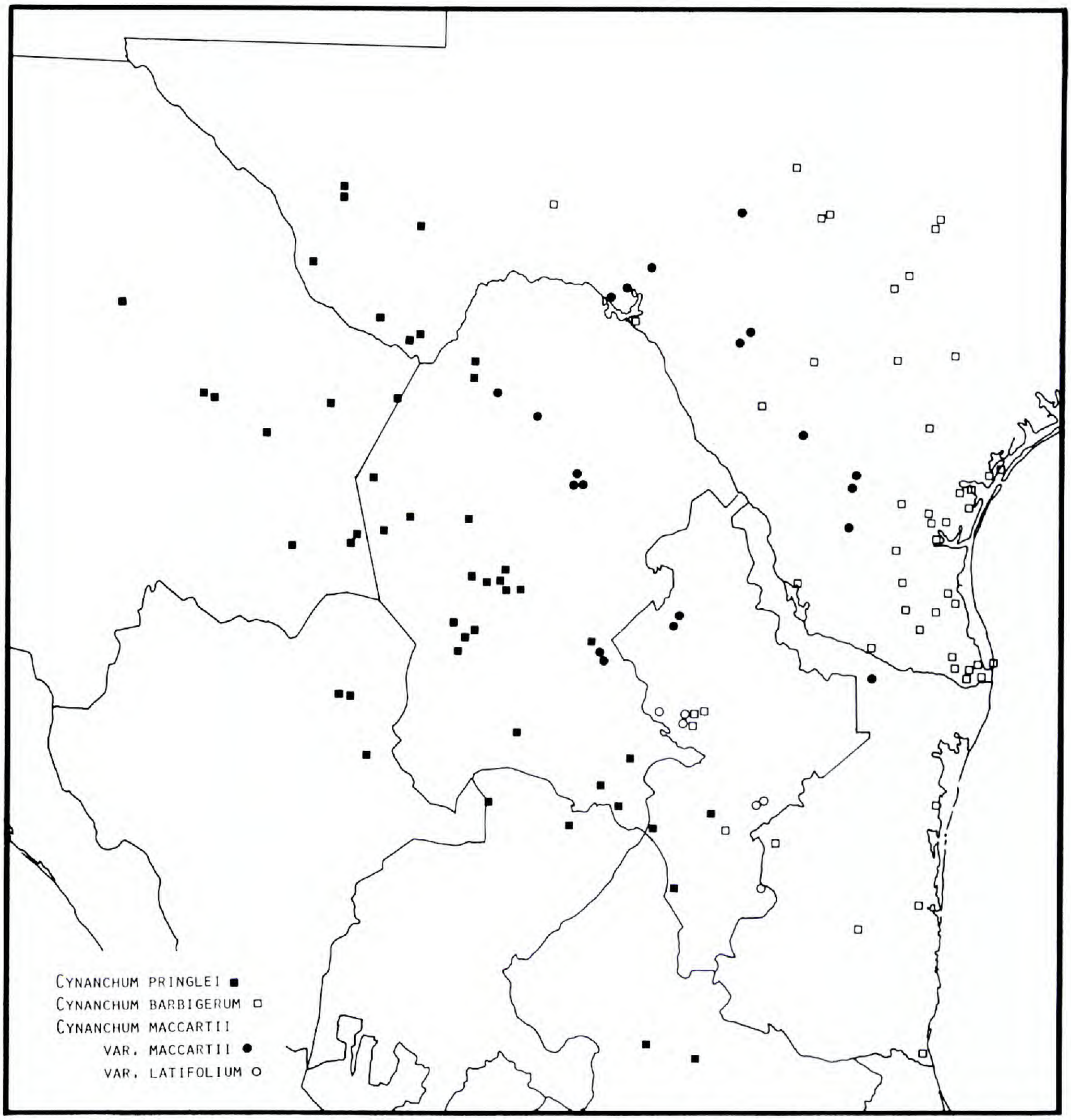

Fig. 2. Distribution of *Cynanchum pringlei*, *C. barbigerum*, *C. maccartii* var. *latifolium*, and *C. maccartii* var. *maccartii* in Texas and adjacent México.

long, 5 – 5.5 mm wide, glabrous, smooth; seeds ca 6 mm long and wide; coma 2 – 2.5 cm long, white.

KEY TO VARIETIES OF CYNANCHUM MACCARTII

A. Leaves oblong-lanceolate to lanceolate, 2.5 – 7(– 10) mm wide; flowers 2.2 – 3.0 mm long; corolla tubes 0.5 – 0.7 mm long; corolla lobes uniformly puberulent inside with hairs 0.03 – 0.1 mm long . . . . . *C. maccartii* var. *maccartii*

AA. Leaves oblong-ovate, (6.5 –)7 – 15(– 17) mm wide; flowers 3 – 4.2 mm long; corolla tubes 1 – 1.5 mm long; corolla lobes puberulent-papillose throughout except for hairs to 0.2 mm long near tip . . *C. maccartii* var. *latifolium*

CYNANCHUM MACCARTII Shinners var. MACCARTII, Sida 1(6):360. 1964, based on *Metastelma palmeri* S. Wats. Proc. Amer. Acad. Arts 18:115. 1883. *Cynanchum palmeri* (S. Wats.) Shinners, Field & Lab 19:65. 1951. [non *Cynanchum palmeri* (S. Wats.) Blake 1917, based on *Pattalias palmeri* S. Wats.]. TYPE: TEXAS. Webb Co.: Laredo on the Rio Grande, Aug 1879, *E. Palmer 824* [LECTOTYPE: (A type was mechanically implied by Standley (1924) as the first among four specimens cited by Watson. This, however, is contrary to International Code of Botanical Nomenclature Art. 8.1. However, the same specimen is accepted here as lectotype as it fits the protologue well) GH!]

Stem internodes glabrous, rarely pubescent in one line with decurved hairs 0.2 − 0.3 mm long; leaves linear-lanceolate to lanceolate, oblong-lanceolate, (12 −)16 − 33(− 50) mm long, 2.5 − 7(− 10) mm wide; flowers 2.2 − 3 mm long; corolla tubes 0.5 − 0.7 mm long; corolla lobes uniformly puberulent inside with hairs 0.03 − 0.1 mm long.

Distinguished from *Cynanchum barbigerum* and *C. pringlei* by the much shorter somewhat matted, thickened hairs on the inner surface of the corolla lobes and from *C. maccartii* var. *latifolium* by the characters given in the key. Occurring in southern Edwards plateau across the south Texas plains from Kimble south to Val Verde, Uvalde, La Salle, Duval and Starr counties in Texas south to eastern Coahuila (Muzquiz, Cuesta de Plomo, Rincón de Maria, Sierra de Gavia), northern Nuevo León (Bustamente), Tamaulipas (near Reynosa), (Fig. 2), from 340 − 1400 m, flowering from May to October. The plants are relatively uniform in their characteristics. One specimen (*L.J. Dorr 2359* from Tamaulipas, road to Bustamente 2.7 mi N of Hwy 70) differs from all others in having the single line of hairs on stem internodes as in var. *latifolia* but flowers are short and leaves are relatively narrow.

CYNANCHUM MACCARTII var. **latifolium** Turner ex Henrickson var. nov.

Differt a *C. maccartio* var. *maccartio* internodiis puberulis constanter foliis magis oblongo-ovatis versus ovatum (6.5 −)7 − 15(− 17) mm latis [non 2.5 − 7(− 10) mm latis] et floribus 3 − 4.2 mm longis (non 2.2 − 3 mm longis) tubis corollarum 1 − 1.5 mm longis (non 0.5 − 0.67 mm longis).

Stem internodes always pubescent in one line with decurved hairs 0.2 − 0.3 mm long; leaves oblong-ovate to ovate, (10 −)15 − 32 mm long, (6.5 −)7 − 15(− 17) mm wide; flowers 3.0 − 4.2 mm long; corolla tubes 1 − 1.5 mm long; corolla lobes 2 − 2.5 mm long, 0.8 − 1.1 mm wide, closely puberulent-papillose inside along margins with hairs 0.1 mm long, but more strongly villous with hairs to 0.2 mm long near tip.

TYPE: MÉXICO. NUEVO LEÓN, Las Anacuas, Mcpio. Linares, 640 m, 5 Aug 1980, *Hinton 17935* (HOLOTYPE: TEX!).

The above variety differs from *C. maccartii* var. *maccartii* mainly in the

broader, more oblong-ovate to ovate leaves, in the consistently vestitured stem internodes and in the larger flowers having longer corolla tubes and longer and denser hairs on the inner tips of the corolla lobes. It appears as an allopatric variety found in the eastern foothills of the Sierra Madre Oriental near Monterrey and southward towards Linares. In all other technical features of the flowers it agrees well with the typical variety.

Additional collections. MÉXICO. NUEVO LEÓN: Sierra Madre above Monterrey, 17 Aug 1903, *C.G. Pringle 11841* (LL, TEX); Sierra Madre, Monterrey, 23 Jul 1933, *C.H. & M.T. Muller 188* (TEX); xeric west wall of Cañon de Potrero Redondo, Mcpio. de Villa Santiago, 4 Jul 1935, *C.H. Muller 2099* (TEX); Las Anacuas, Mcpio. Linares, 670 m, 12 May 1980, *Hinton 17776* (TEX).

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A TAXONOMIC REVISION OF *VAUQUELINIA* (ROSACEAE)

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ABSTRCT

Vauquelinia is a genus of small trees and shrubs endemic to Mexico and southwestern United States. Due to considerable overlap in vegetative characteristics, the 11 taxa are grouped into three species: *V. australis* of Oaxaca and Puebla; *V. californica* with four subspecies, subsp. *californica*, subsp. *pauciflora*, subsp. *sonorensis*, and subsp. *retherfordii* from Arizona and New México south to Durango, Coahuila and Baja California, and; *V. corymbosa* with 6 subspecies, subsp. *corymbosa*, subsp. *heterodon*, subsp. *angustifolia*, subsp. *karwinskyi*, subsp. *saltilloensis*, and subsp. *latifolia* from Hidalgo, Querétaro north to Nuevo León, Coahuila, and trans-Pecos Texas. Data on leaf, flower anatomy, as well as floral vascularization are also included.

INTRODUCTION

The genus *Vauquelinia* is comprised of eleven taxa of evergreen, sclerophyllous, shrubs to small trees native to the arid, and semi-arid lands of México and adjacent United States from Puebla-Oaxaca north to Baja California, Arizona, New Mexico, and trans-Pecos Texas. The genus is here treated as composed of three species, one species having four subspecies, another with six subspecies, and the third without infraspecific divisions.

The genus *Vauquelinia* was erected by Humboldt and Bonpland (1807) in their *Plantae Aequinoctiales* based on a collection from near Actopan, Hidalgo. The genus was named, at the urging of José Francisco Correa de Serra, a Portuguese botanist, for Frenchman Nicolas Louis Vauquelin (1763-1829), student and associate of Fourcroy, later distinguished chemist, physicist, and author, whose discoveries in chemistry carried over into botany. Hence the genus is to be cited as *Vauquelinia* Humboldt et Bonpland, or, following the recommendation presented in article 46E of the International Code of Botanical Nomenclature (Voss et al. 1983), *Vauquelinia* Correa ex Humboldt et Bonpland. The new genus contained one species, *V. corymbosa*, and the genus remained monotypic for 40 years. Botanical activity in the frontiers of the United States added a second

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species, *V. californica*, from mountains near the Gila, Arizona. A third species, *V. karwinskyi*, was named in 1879 by the Russian botanist Maximowicz from collections of Karwinsky west of Ciudad Victoria, Tamaulipas. Rydberg (1908) was the first to enumerate the genus in the Flora of North America, where he recognized four species, the above three taxa and a newly described *V. angustifolia* from the state of Chihuahua, México. Soon after, four more species were described: *V. potosina* from San Luis Potosí, México; *V. australis* from Puebla, México; *V. pauciflora* from northern Sonora near New Mexico; and *V. latifolia* from Tamaulipas, México.

Standley (1922) recognized six species in his *Trees and Shrubs of Mexico*, all of the above taxa with the exception of Rydberg's *V. angustifolia* and his recently described *V. potosina*, both of which he placed in synonymy. Since Standley's treatment two additional taxa have been described from the Chihuahuan Desert Region by I.M. Johnston in the 1940's: *V. retherfordii* from southwestern Coahuila, México; and *V. heterodon* from eastern Coahuila. The work presented here represents the first systematic treatment of the genus in over 60 years. We here describe two new taxa and recognize a total of eleven taxa in three species.

In the above noted taxonomic treatments, the taxa of *Vauquelinia* have been distinguished on the basis of various vegetative characteristics, namely leaf shape, size, serration, and vestiture. Indeed, as in several other woody genera of Rosaceae (e.g. *Cercocarpus*, *Holodiscus*, *Malacomeles*, *Rosa*, and *Spiraea*) as well as in *Arctostaphylos*, *Arbutus*, *Comarostaphylis*, *Ceanothus*, *Ptelea*, and *Quercus*, taxa of *Vauquelinia* are relatively uniform in their flower and inflorescence structures, forcing taxonomists to rely heavily on vegetative features. In *Vauquelinia* each population has a characteristic or typical leaf size, shape, and serration along with an often perplexing amount of leaf variation that frequently falls well outside the expected range of variation. Some of this aberrant leaf variation is genetically based and represents extremes in genetic variation in a population. For example, plants surviving in extreme arid microhabitats commonly have smaller leaf blades—i.e., representing the survivors in a process of strong natural selection on seedlings. Similar reduced blades have been encountered when plants are under heavy grazing pressures. Other plants, perhaps occurring in more favorable microhabitats, have larger or more coarsely serrate leaf blades, and this variation must be incorporated into the range of variation of the taxon. Even on one plant, the first- and last-formed leaves of a season's increment are usually smaller and sometimes will differ in shape and serration from the others on the same stem. The average leaf shape, size, and marginal toothing and other features will also vary between disjunct

populations. In many instances populations are confined to slightly more mesic canyons in arid mountains where they occur as relicts of a perhaps more widespread distribution during the Holocene. Variation in leaf vestiture is also encountered.

It is, however, misleading to state that no taxonomically useful characteristics occur in flowers and inflorescences. Both quantitative and qualitative differences do occur in flowers involving size differences in petals and sepals, and the presence or absence of such features as glands along the sepal margins. However, as flowers are not present on all specimens it is difficult to assess the variation in these characters and to use these characters for identification. Generally we find there is considerable variation in floral characteristics as well. We therefore continue to emphasize vegetative (leaf) characters in our treatment as: 1) leaves are present on all specimens and; 2) the majority of plant collections can readily be identified on this basis. To accommodate the often wide range of leaf variation we discuss and present illustrations of many of these aberrant leaf types.

It has been somewhat disconcerting to find that the broad range of leaf variation encountered in some populations of *Vauquelinia*, as in taxon *corymbosa*, includes types completely referable to other taxa, e.g., taxon *heterodon*, and likewise to find occasional *heterodon*-like as well as *angustifolia*-like leaf characteristics in populations of taxon *karwinskyi*. It is unknown whether these extreme morphotypes indicate past introgression between these now disjunct taxa or are merely representative of the great potential of genetically-based variation in these apparently outcrossing taxa. But because of this wide degree of variation inherent in these taxa it becomes difficult to recognize them as distinct species. Whether they also contain isolation mechanisms that would allow them to retain their differences should they ever become sympatric is also unknown, but the diversity encountered in the taxa indicates that they may interbreed freely with other such taxa.

Because of the overlap in morphological characteristics and the lack in true qualitative differences separating these taxa, we recognize only three species in the genus and relegate other taxa to subspecific rank. The three species recognized include: 1) *Vauquelinia australis* Standl. (with no subspecies), occurring south of the transverse volcanic belt in the states of Puebla and Oaxaca, México and characterized by mostly oblanceolate, bicolored leaves with revolute, closely serrate margins; 2) *Vauquelinia corymbosa* Humb. et Bonpl., with six subspecies occurring along the Sierra Madre Oriental axis from Hidalgo-Querétaro north to Nuevo León-Tamaulipas and spilling into the Chihuahuan Desert to trans-Pecos Texas

and eastern Chihuahua characterized by ovate to linear, mostly glabrate leaves mostly with relatively coarse marginal serrations; and 3) *Vauquelinia californica* (Torr.) Sarg., with four subspecies occurring from Arizona and New Mexico south to Baja California and along the eastern slopes of the Sierra Madre Occidental with disjunct populations in central Coahuila characterized by lanceolate to linear, glabrate to bicolored leaves with relatively fine marginal crenulations to serrulations. We feel this is the most supportable taxonomy in which the species are reasonably well defined both morphologically and geographically and the subspecies are defined on the basis of quantitative differences in leaf shape, toothing, and vestiture, as well as geographical distribution. In all but one instance the subspecies are allopatric, occurring mostly in widely disjunct population series. In areas where subspecies of *V. corymbosa* and *V. californica* apparently have been sympatric in the past, populations showing hybrid characteristics occur at present.

Fossils of leaves considered to belong to *Vauquelinia* are recorded from two fossil floras in the western United States. In the mid-Tertiary Florissant beds in Colorado (lower to mid-Oligocene—30 mybp.) MacGinitie (1953) reports two Vauquelinias: *V. liniara* MacGinitie, with linear leaves considered to be referable to *V. angustifolia* and; *V. coloradensis* (Knowlton) MacGinitie with more obovate leaves considered closest to *V. californica*. In the mid to upper Eocene Green River flora MacGinitie (1969) reports one species *V. comptonifolia* (Brown) MacGinitie that he again refers to *V. californica*.

Recent discussions have questioned the relationships of *Vauquelinia* within the Rosaceae. In traditional classification schemes the North American *Vauquelinia*, *Lindleya*, *Lyonothamnus* and the South American *Quillaja* and *Kageneckia*, as well as the Asiatic *Exochorda* have constituted the subfamily Spiraeoideae, tribe Quillajeae, characterized by woody habits, five carpels opposite the sepals, winged seeds and either capsular or follicular fruits (Maximowicz 1879). Cytological studies by Goldblatt (1976) have suggested that *Vauquelinia* ($n = 15$) and *Lindleya* ($n = 17$) should be transferred from the Spiraeoideae ($x = 9$) to the paleoamphiploid subfamily Maloideae = Pomoideae) ($x = 17$), while *Exochorda* ($n = 8$) should be transferred to the Prunoideae ($x = 8$) and *Lyonothamnus* ($n = 27$) should be retained in the Spiraeoideae. He further suggests that *Kageneckia* ($n = 17$) and *Quillaja* ($n = 14$) are primitive in the family and should constitute a separate subfamily. The work of Sterling (1966) on comparative anatomy of the carpel of the Rosaceae independently noted the similarities in ovaries of *Vauquelinia* and *Lindleya* to those of the Maloideae. *Vauquelinia* is most closely related to *Lindleya*, and the latter differs from

Vauquelinia in a large number of features, including: 1) completely united carpels that form spheroid, five-celled, woody capsules; 2) paired, epitropic (not basal) ovules; 3) usually solitary, larger, showier flowers; 4) chromosome number (see above); 5) smaller, less coriaceous leaves; and a large number of additional characteristics.

The emphasis in this treatment is largely morphological. Our descriptions are based on extensive and intensive field and herbarium observations. We present detailed descriptions of the anatomy of vegetative, floral and fruiting structures to serve as a database for comparative studies. We also discuss the question regarding relationships of *Vauquelinia* in the Rosaceae and present keys for identification and descriptions of all taxa in the genus. No attempt is made here to indicate phenetic or phylogenetic relationships between the taxa other than that inherent in our classification.

MATERIALS AND METHODS

Herbarium specimens were borrowed from A, ARIZ, ASU, CAS, ENCB, DS, F, GH, JEPS, LL, MO, MEXU, MICH, NY, POM, RSA, SD, TEX, UC. All taxa were observed in the field during various trips in the late 1970's and in connection with the Chihuahuan Desert Flora project. Anatomical studies incorporated standard paraffin techniques for production of serial sections of leaves and flowers. SEM photomicrographs were taken with a Jeol JSM T-200 at the biology department of California State University, Los Angeles,. All plant measurements were made from dried materials unless otherwise noted.

RESULTS

COMPARATIVE ANATOMICAL STUDIES: In the section that follows we present detailed, though brief, baseline descriptions of the anatomy of stems, leaves, flowers, fruits, and seeds. Pertinent comparative data between taxa of *Vauquelinia* are emphasized. We feel this information will be important in anatomical comparisons with other potentially related genera.

Growth Habits:Taxa of *Vauquelinia* range from multi-stemmed shrubs (fig. 1a) to single-trunked trees. Arboreal taxa occur in more mesic montane habitats, or where they have been free of various perturbations. In more arid regions plants commonly occur in rocky habitats, occasionally growing in crevices. Plants may die back during extreme droughts and send up new basal shoots in favorable times. Williams (1971) notes the adverse effects of fire on growth habits of plants in southern Arizona and the tendency of the plants to produce basal sucker shoots after fire damage.

Stem Structure: Young stems are covered with a dense to thin vestiture of crinkled, uniseriate, unicellular trichomes that is generally lost after the first year. The outer cortex contains collenchyma and many tannin-containing cells, and the inner bark contains large initial bundles of phloem fibers. Secondary phloem produces masses of fibers that eventually are built into the periderm. Primary vascular tissue is in a closed cylinder.

Fig. 1. Growth habit, leaves, flowers of *Vauquelinia*. a-b.—*V. californica* subsp. *californica*. a.—Typical growth habit of small tree ca 2.5 m tall with multiple basal stems. From Catalina Mountains, Pima County, Arizona. b.—Leaves are erect-ascending, slightly folded along midrib. (*Henrickson 20289*). c-d.—*V. corymbosa* subsp. *heterodon*. c.—Leaves and corymbose inflorescences. d.—Flowers. (*Henrickson 16171*) Scales in b-d = 1 cm.

Pith lignifies in time. The first phellogen develops in the outermost cortex layer immediately beneath the epidermis. Older stems have a smooth, gray to dark gray bark. In older trunks outer bark peels, becomes vertically plaited, and generally is dark gray to black in color.

Nodal Vascularization: Nodal vascularization in *Vauquelinia* is three-trace, tri-lacunar, with lateral traces separating from the vascular cylinder slightly below the medial vascular trace. The three traces join in the lower, flattened portion of the petiole above the point of eventual abscission and continue up the petiole-midrib as a single, massive, crescent-shaped trace. Small stipular traces diverge from the outer margins of the lateral trace at the petiole base. Axillary bud traces separate from the inner margins of the medial gap and join shortly above.

Leaf Anatomy: Leaf blades are coriaceous, bifacial, and range from 0.25 − 0.52 mm in thickness. New leaves are produced in the spring on shoots that terminate in an inflorescence. Older leaves persist until after the new leaves have matured, generally abscissing from mid-late summer to winter. Leaf-blades are flat or slightly folded along the midrib with margins flat or very slightly decurved (fig. 1b-c), or in *V. australis* strongly revolute. Epidermis cells on both surfaces are pentagonal to polygonal (Dilcher 1974) with straight anticlinal walls. Those over the mid to tertiary series of vascular bundles (those with bundle sheath extensions) are elongated parallel to the subtending bundle, rectangular with straight or oblique end walls. Cuticles range from (4.5 −)7 − 14 μm in thickness, are typically thicker on the upper surface, and lack cuticular relief, though the outer tangential walls may be somewhat thickened medially, forming low papillae. The lower epidermis of *V. corymbosa* subsp. *corymbosa* and subsp. *heterodon* often develops waxy surface deposits, consisting of localized masses of vertically-oriented platelets (fig. 2c − d). They were not seen in other taxa. Leaves of *V. corymbosa* subsp. *latifolia* are distinctly glaucous on both surfaces. *Vauquelinia australis* and some subsp. of *V. californica* are variously vestitured on the lower surface and around the midrib of the upper surfaces, as well as on stems, inflorescences, etc. Trichomes in all these taxa are cylindrical, tightly curled to crinkled, 6 − 7 μm in diameter with thickened walls that leave a reduced lumen to 2 μm in thickness (fig. 2b).

Stomata are restricted to the lower epidermis, are randomly oriented, and lacking over vascular bundles with bundle sheath extensions. Guard cells range from 25 to 34 μm in length, are superficial, accompanied by a thinning of cuticle that forms a weak exterior ledge, and are subtended by 6 − 9(− 10) subsidiary cells in one series (cyclocytic). In surface view subsidiary cells overlap the guard cells.

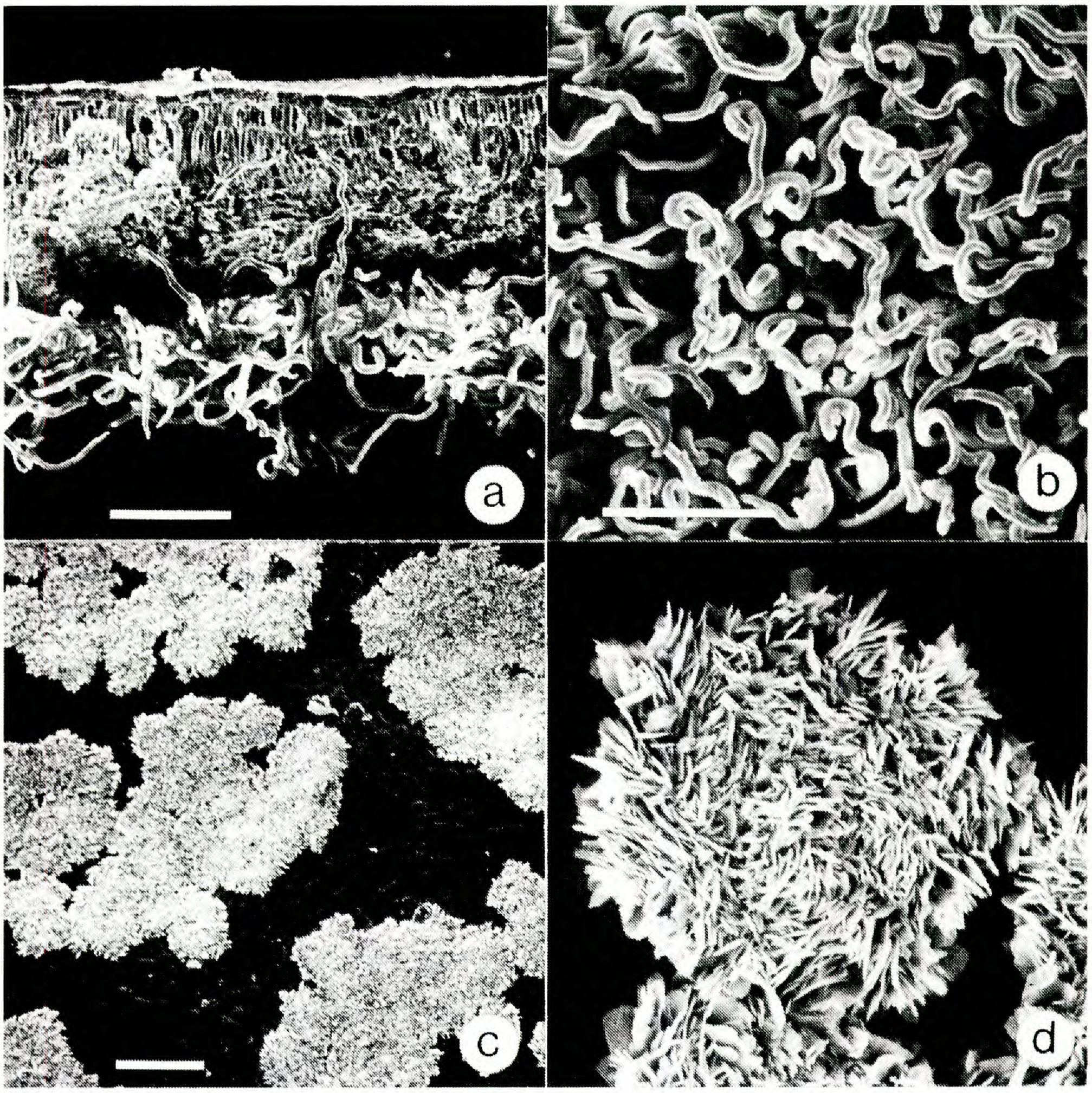


Fig. 2. Scanning electron micrographs of leaves of *Vauquelinia*. a.—*V. californica* subsp. *sonorensis*. Cross section of leaf showing dense abaxial vestiture. (*J.M. Tucker 2427*). b.—*V. californica* subsp. *retherfordii*. Abaxial leaf vestiture showing characteristic crinkled trichomes. (*Stanford et al. 87*). c-d.—*V. corymbosa* subsp. *c*. Lower leaf surface showing distinctive accumulations of vertical wax platelets. (*C. Mason 2621*). Horizontal bars in a-c = 0.1 mm, central mass in d is ca 0.1 mm in diameter.

As seen in cross sections, the upper epidermis is commonly subtended by a single (rarely double in *V. c.* subsp. *karwinskyi*) hypodermal layer usually distinguished by inclusions of saffranin-staining, tannin-like substances. In most species hypodermis is not complete but merely represents broad lateral extensions of the bundle sheath extensions (fig. 3a). A less well developed hypodermal layer may also occur next to the lower epidermis, again associated with bundle sheath extensions, but here it is interruped by substomatal chambers. Mesophyll consists of (1−)2−3(−4) tightly packed palisade layers dorsally and a relatively

dense (fig. 3a) to moderately open (fig. 3b), vertically-arranged series of cells ventrally. These ventral cells are sometimes tightly arranged in a palisade-like configuration, particularly under vascular bundles without lower bundle sheath extensions (fig. 3a), or immediately adjacent to these extensions. The midrib and secondary, tertiary, and in some taxa the 4th

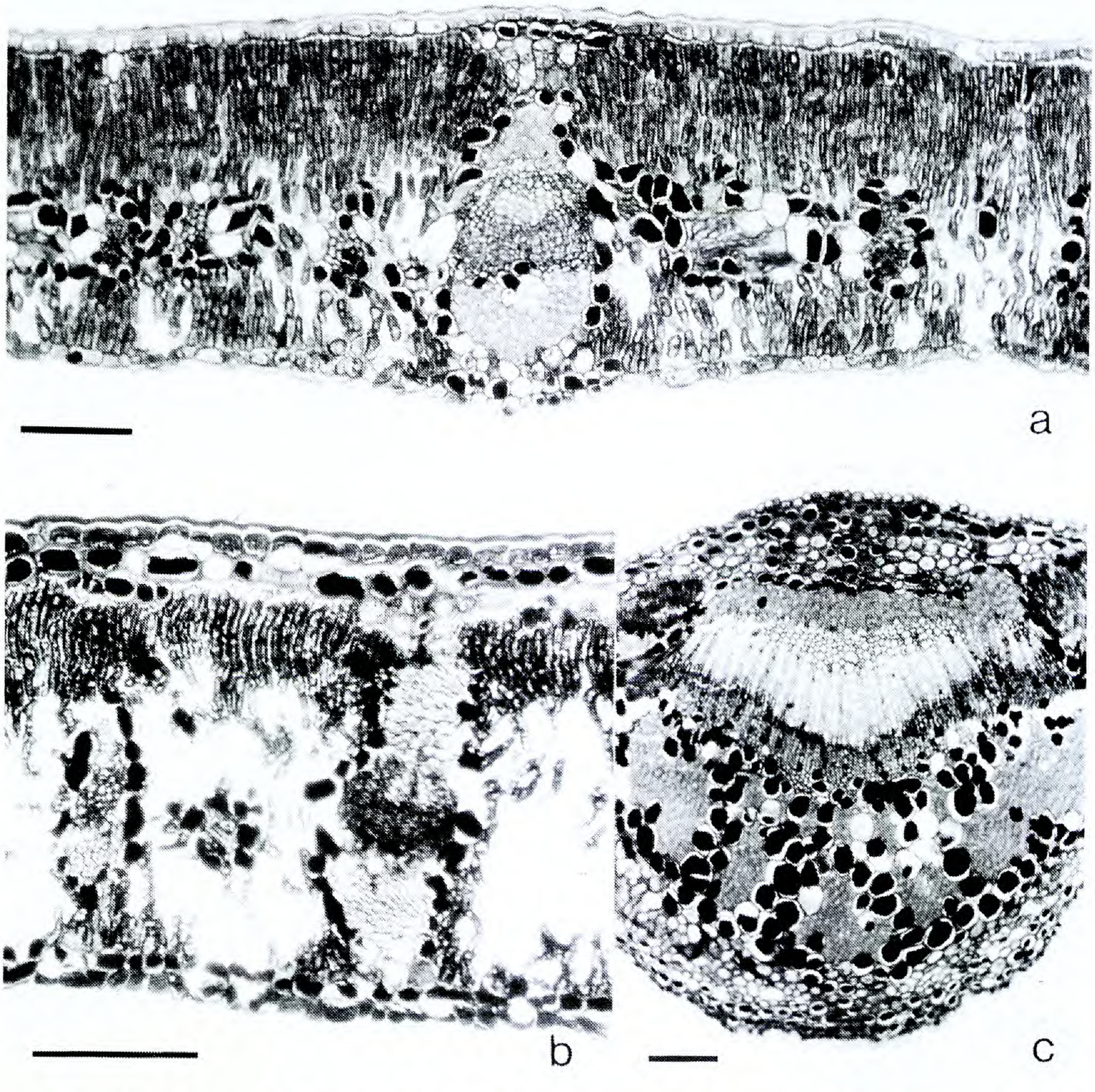


Fig. 3. Leaf structure in *Vauquelinia*. a.—*V. californica* subsp. *californica*. Cross section of leaf, showing multiple palisade layers. Largest vascular bundle has bundle sheath extension and large bundles of fibers opposite xylem and phloem. Bundle sheath extensions are absent in smaller veinlets. Note tannin-filled hypodermal and bundle-sheath cells. Leaf is ca 0.3 mm thick. (*Hess & Wilhelm 4253*). b.—*V. corymbosa* subsp. *heterodon*. Cross section of leaf showing distinct hypodermal layers and very open mesophyll. Note masses of fibers on both sides of vascular bundles. Leaf is ca 0.3 mm thick. (*Henrickson 16971*). c.—*V. corymbosa* subsp. *angustifolia*. Cross section of midrib showing extensive series of fiber bundles opposite phloem. Note dark, tannin-filled cells. Section is to ca 0.83 mm thick. (*Henrickson 15075*). Horizontal bars all = 0.1 mm.

and 5th series of vascular bundles have bundle sheath extensions continuing to both epidermises. The vascular bundles and extensions are surrounded by a single-layered bundle sheath typically distinguished by tannin-like inclusions (fig. 3a—b). The midrib, secondary, and tertiary vascular bundles all have active vascular cambia revealed by the orientation of xylem and phloem cells, and have two well developed bundles of fibers, the larger opposite the phloem and representing primary phloem fibers, the other smaller series opposite the xylem (fig. 3a—c). Between the vascular bundles and hypodermis are parenchyma cells typically packed with cuboidal, prismatic, or rather irregularly shaped or druse-like crystals.

The midrib vascular bundle (fig. 3c), as noted previously, is very large, crescent-shaped, and with an obvious functional vascular cambium. It has a series of large fiber bundles outside the phloem separated by series of large, tannin-filled cells. The similar, continuous series of fibers opposite the xylem is smaller. The tissue outside the fibers consists of parenchyma and lacunar collenchyma, some with crystals, and some with tannins (dark staining cells). In *V. californica* veinlets of the 4-5 series lack bundle sheath extensions and consist of only xylem and phloem surrounded by a single bundle sheath layer. The smallest veinlets contain only xylem. In the thickly coriaceous leaves of *V. corymbosa subsp. latifolia*, however, bundle sheath extensions occur on even the 4—5 series of vascular bundles (fig. 4a). In this instance the pattern of vascularization is reflected in fiber bundles opposite the xylem and opposite the phloem. In cleared whole leaf material, the xylem fiber series could be separated completely from the phloem fiber series.

As seen in leaf clearings (fig. 4), venation is pinnate and semicraspedodromous (Dilcher 1974). Midveins are straight and massive, and generally constitute 4—5 percent of the leaf-blade width. Secondary veins are irregularly divergent from the midvein at acute angles, often paralleling the midvein before the point of divergence (fig. 4d), either straight or upcurved distally, sometimes with the distal secondary veins of the leaf blade more acute than the mid-lower veins. Secondary veins may variably fuse and branch before the margin (not all terminate in marginal teeth) but join with superadjacent veinlets through prominent marginal fimbriae or branches. All species are distinguished by series of irregular, composite intersecondary veins originating from the midvein that are usually moderately prominent, straight near the midvein but are more zigzagged, and evidently composed of tertiary veins near the margin (fig. 4). The intersecondary veins are highly variable in development, sometimes being prominent and fusing with secondary veins, and at other times gradually

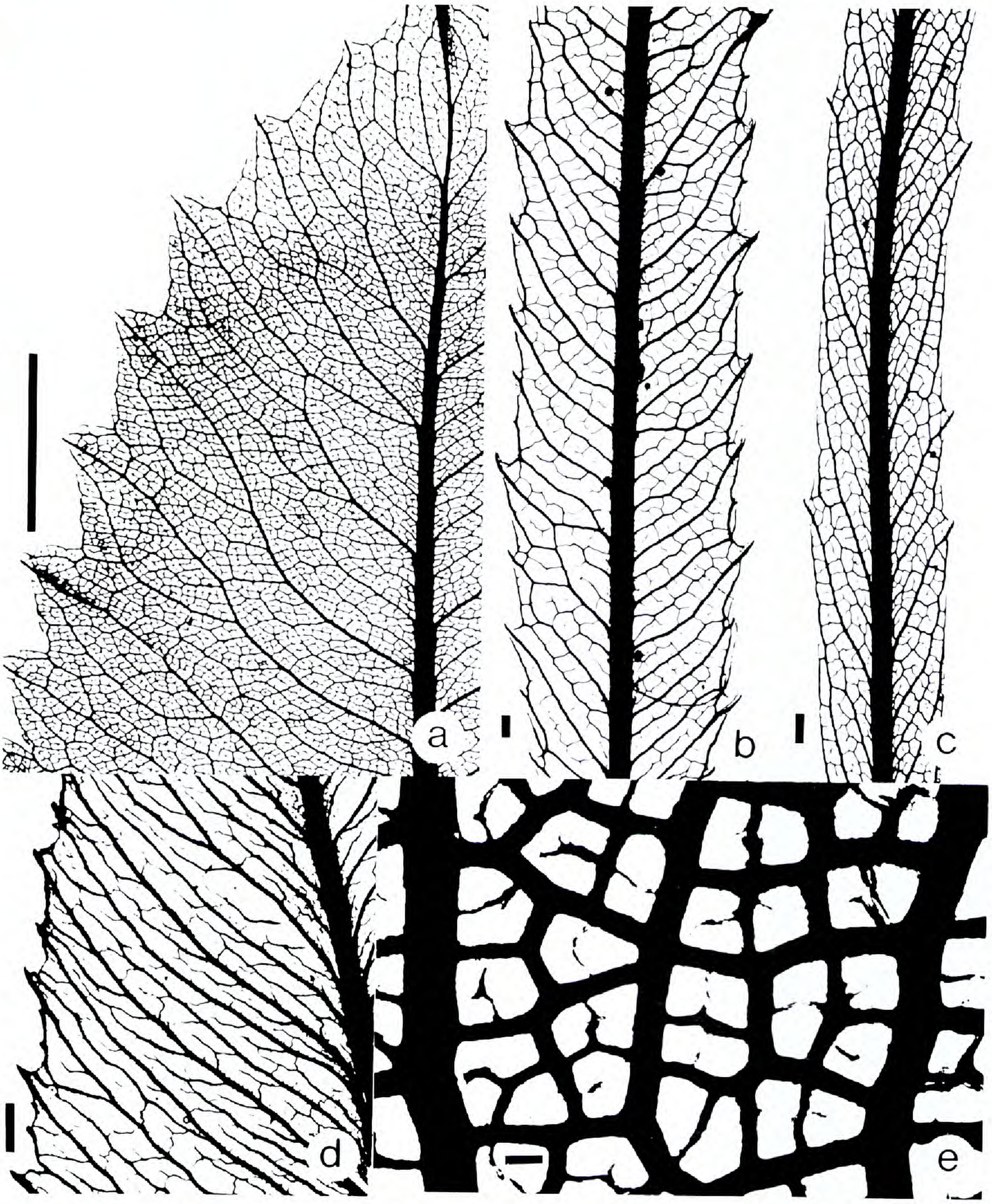


Fig. 4. Cleared leaves of *Vauquelinia* showing stained venation. a.—*V. corymbosa* subsp. *latifolia*. In this taxon the midrib to 5th series of veinlets all have bundle sheath extensions with 2 series of fibers. (*Henrickson & Hess 19235*). b.—*V. corymbosa* subsp. *heterodon*. Note intersecondary veinlets. Leaf is to ca 10.5 mm wide. (*Henrickson 16871*). c.—*V. corymbosa* subsp. *angustifolia*. Leaf is to 4.3 mm wide. (*Henrickson 15075*). d.—*V. californica* subsp. *californica*. Note differences in minor venation. (*Hess & Wilhelm 4253*). e.—*V. corymbosa* subsp. *corymbosa*. Enlargement of secondary and minor venation. Two largest vertically-oriented veins are secondary veins, the medial large vein is an intersecondary vein. Bundle sheath fiber masses extend to quaternary veins but not to 5th series. (*Hess & Wilhelm 4371*). Horizontal bars in a = 1 cm; in b-d = 0.1 mm; in e = 0.01 mm.

diminishing near the leaf-blade margins. They are least developed in collections of *V. californica* subsp. *californica* (fig. 4d). Tertiary veinlets usually arise alternately, more or less at right angles (fig. 4a–c, e) or sometimes at acute angles (fig. 4d) to the secondary veins; they are variously joined (percurrent) and forked to a 4th or 5th degree of branching with intercostal areas producing series of triangular to polygonal orthogonal reticula (fig. 4e). Areoles are small, well developed, occasionally imperfect, ranging from triangular to polygonal in outline and have simple or variously once (-twice) branched veinlets.

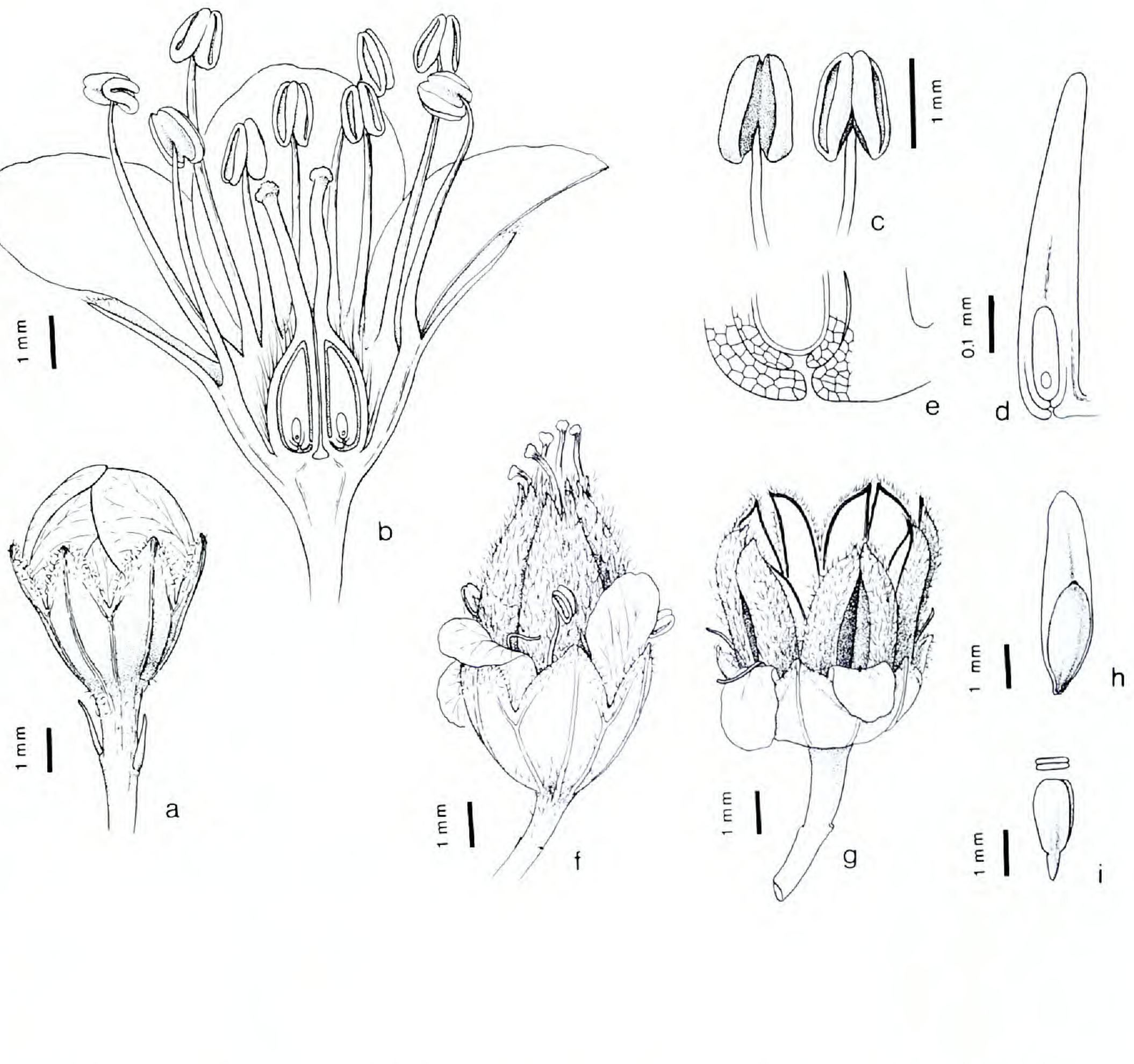
Inflorescences: Flowers are borne in compound corymbs (figs. 1c, 10a). The lowermost peduncles are subtended by reduced leaves (fig. 10a). Upper bracts and bracteoles are membranous, linear-subulate, and commonly beset with marginal glands.

Flowers: Hypanthia: Pedicels terminate in thick-walled, coriaceous hypanthia (fig. 5b). In bud stages the hypanthium and sepals may be densely vestitured, but they are generally glabrate with age. The basal outer hypanthia are commonly pentagonal, with the angles opposite the mid-sepal line. The inner hypanthium surface around the ovary is nectariferous and contains many stomata.

Sepals: The hypanthium terminates in five deltate, coriaceous sepals with narrow, membranous margins. In bud the sepals are valvate (fig. 5a), often strongly vestitured outside and along the inner margins. This vestiture usually diminishes in extent by anthesis, but a dense marginal tomentum commonly persists. Representative sepal vascularization is shown in fig. 6m. The membranous sepal margins commonly contain series of marginal glands in taxa of *V. californica*. Sepals persist as erect structures around the fruit (fig. 5f–g).

Petals: Petals are white, imbricate in bud but spreading at maturity. Each petal receives a single trace from the hypanthium, but this soon divides and anastomoses above (fig. 6n). Most petals are somewhat oblong to oblong-ovate, oblong-obovate, entire, rounded or sometimes retuse apically and have short, broad claws at their bases. In taxa characterized with strong vestiture they are often densely covered with trichomes where exposed in bud, but the vestiture falls away prior to anthesis. Occasionally some hairs persist at the petal tip at anthesis. In some taxa the petals are caducous, in others they recurve and persist around the fruit (fig. 5f).

Fig. 5. Flowers, fruit and seeds of *Vanquelinia*. a-e.—*V. corymbosa* subsp. *heterodon*. a.—Bud showing two bracteoles, sepals with conspicuous external venation and marginal vestiture, and imbricated petals. b.—Diagrammatic cross section of open flower showing central space between ovaries, styles, position of ovules, hirsute vestiture on exterior of ovaries, stamens, and perianth. c.—Stamens showing anthers in abaxial (left) and adaxial (right) view. (all *Henrickson 16076*). d-e.—Embryo structure.



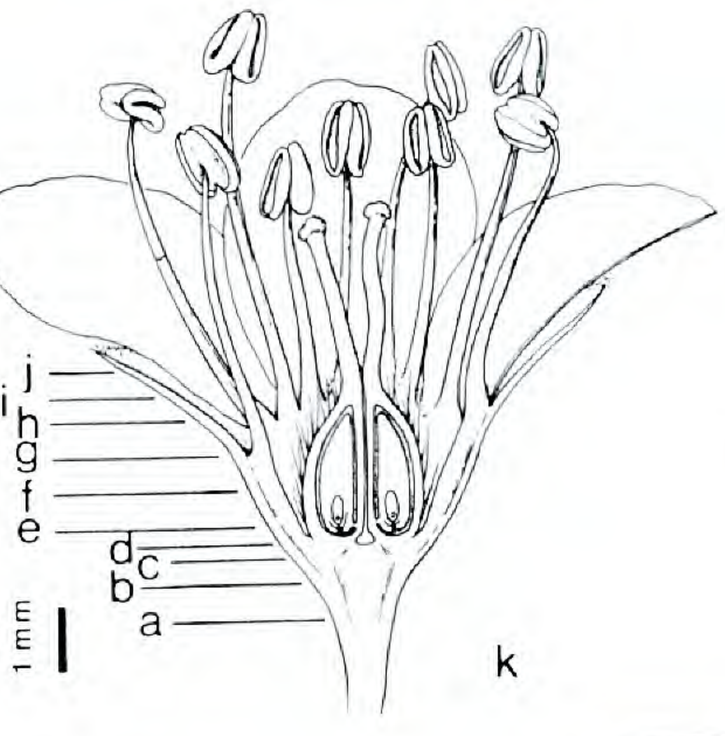
d.—Embryo ca 1.25 mm long with two integuments, tissue above embryo sac stains darkly. Note vascular trace in funiculus. e.—Detail of integuments and micropyle. Embryo sac measures 8 um in width. (*Henrickson 16971*). f-g. Mature fruits of *V. californica* subsp. *sonorensis*. f.—Closed fruit showing sepals, persistent petals, and styles. g.—Open fruit showing persistent sepals, and carpels that separate completely along ventral suture and partway down dorsal suture. Outer walls are hirsute; inner pericarp surfaces are smooth and dry. (*Henrickson 20283*) h-i.—*Vauquelinia californica* subsp. *californica*. h. Seed showing basal embryo and terminal wing. i.—Embryo showing structure and cross section of cotyledons. Magnifications as indicated.

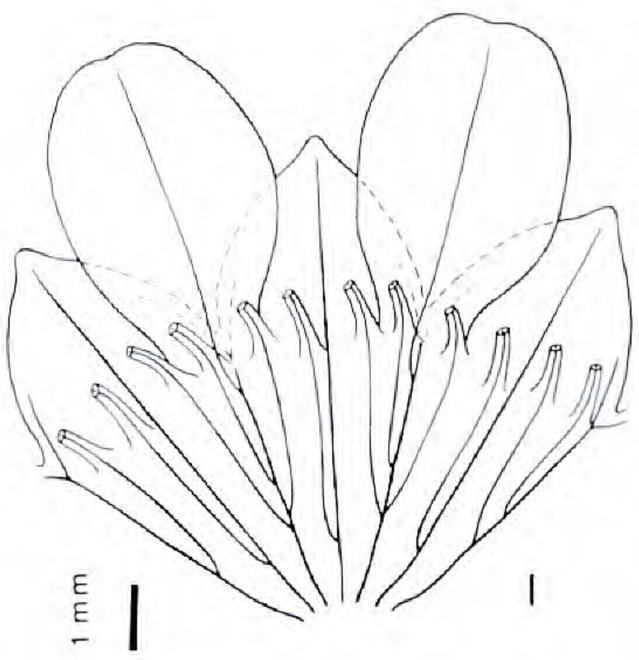
ANDROECIA: Most flowers have 18 – 20 stamens, with 20 the expected number (see floral vascularization section). The stamen series opposite the sepals are separated from the hypanthium slightly before the others, while the three stamens opposite each petal are briefly and marginally adnate to the basal inner petal margin, and their filaments separate more or less simultaneously. Except for the first series, stamens are not produced in distinct whorls. Filaments are subulate, glabrous, white, often abruptly expanded at the base where they may be briefly connate (fig 5b). Anthers are bithecate, tetrasporangiate, glabrous, yellowish-gold, and introrsely dehiscent (fig. 5c). They have glandular tapeta, and the anther-sac walls are three cells thick. Pollen is tricolporate, and prolate. Exine is thin, and the grains commonly collapse when cleared. Sexine sculpturing is tectate, very finely reticulate with 9 – 12 reticula per 5 μm that form into distinct striate patterns that continue across the polar regions (fig. 7d). Cleared pollen measured 23.5 (range 19 – 29) μm in equatorial diameter, 22 (range 17-26) μm in polar diameter.

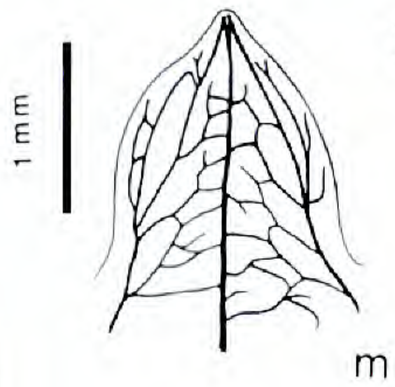
GYNOECIA: The ovary consists of five carpels, is sessile on the receptacle (fig. 5b), and is only slightly adnate at its lower margins to the hypanthium. Each carpel contains two erect apotropous ovules in a single locule (fig. 6g, Sterling 1966). Ovules are elongate, with the terminal portion eventually developing into a seed wing (fig. 5d). Two integuments line the basal micropyle (fig. 5e). The embryo sac forms near the base of the ovary, contained in a crassinucleate nucellus that is surrounded by a single layer of tannin-containing cells. At the ovary base carpels are adnate all along their margins, and their inner (ventral) sutures are usually closed (fig. 7a – b). Above the ovary base the outermost portions of the carpels separate. Each carpel receives three vascular traces, a distinct dorsal trace and two ventral traces that divide into wing and ovule traces at the base of the ovary (fig. 6e – f, Sterling 1966). Both wing and dorsal traces continue into the style (fig. 6j). In fruit additional vascular tissue becomes apparent in the ovary wall. The outer portion of the ovary is strigose, covered with erect, stiff, lignified trichomes. Styles are short, erect, thickened distally, and terminate in truncate to oblique, rounded styles (fig. 5b). Dried styles often persist on the fruit (fig. 6f).

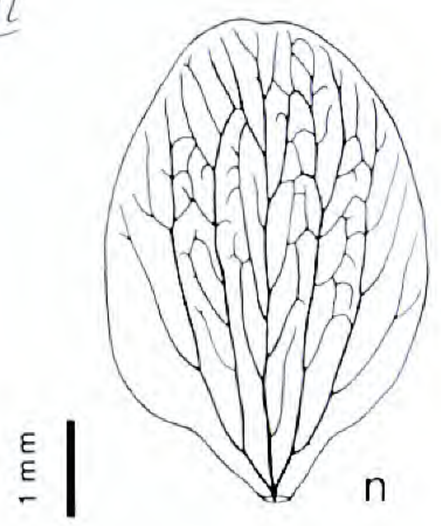
Floral Vascularization: The pattern of flower vascularization was determined from cleared and paraffin-sectioned preserved floral materials of three taxa—*V. corymbosa* subsp. *heterodon*, *V. c. subsp. angustifolia* and *V. californicia* subsp. *retherfordii*. All are basically similar in vascularization pattern, though some minor variations were noted (fig. 6).

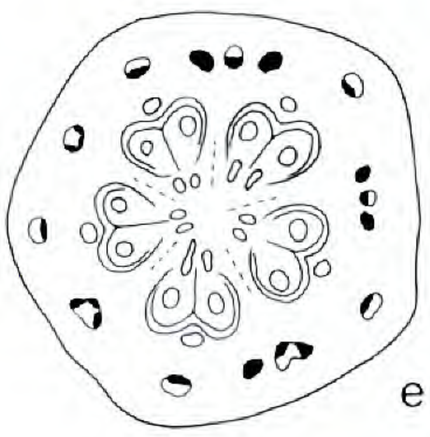
Vascular tissue in the pedicels organizes into a series of 10 peripheral traces that extend centrifugally into the base of the hypanthium or floral

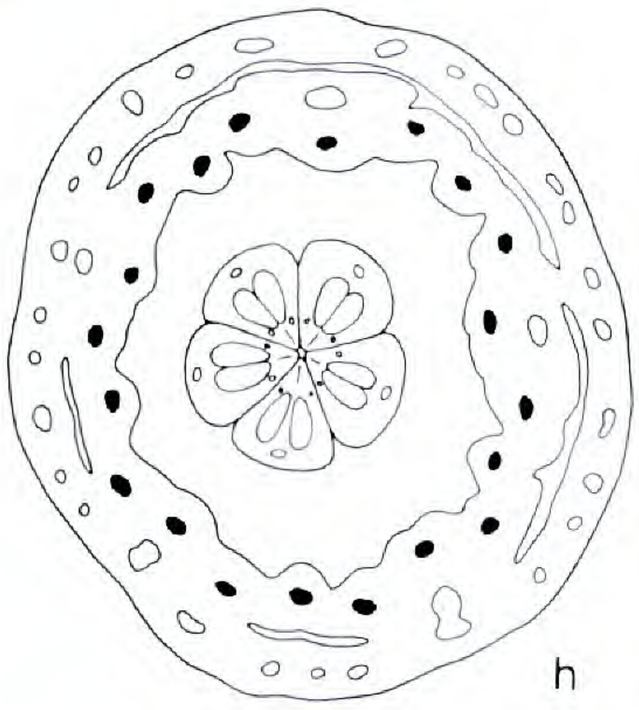


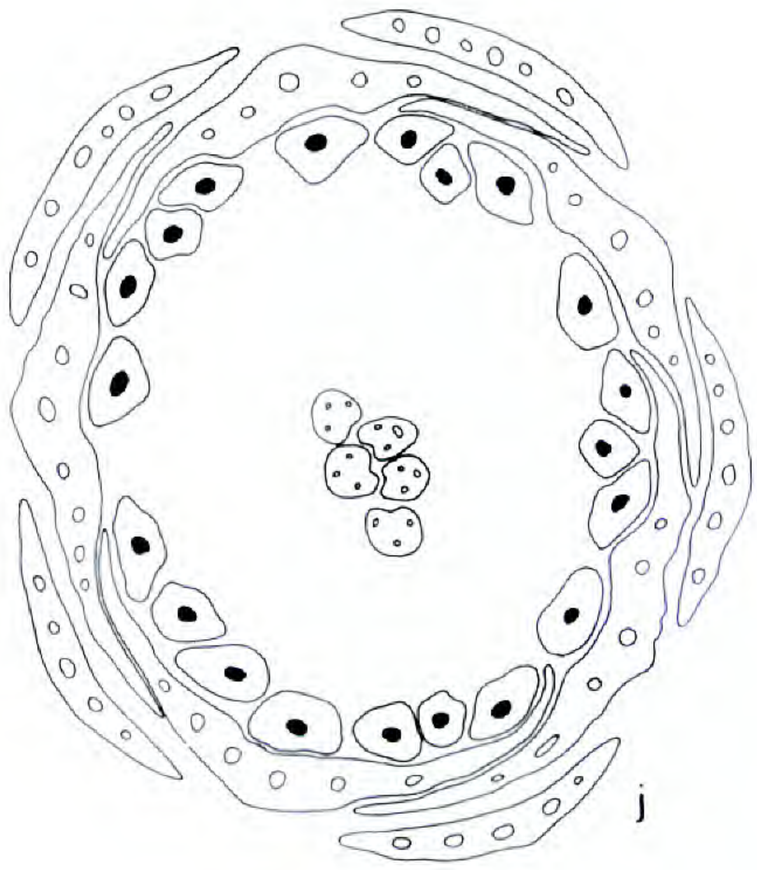


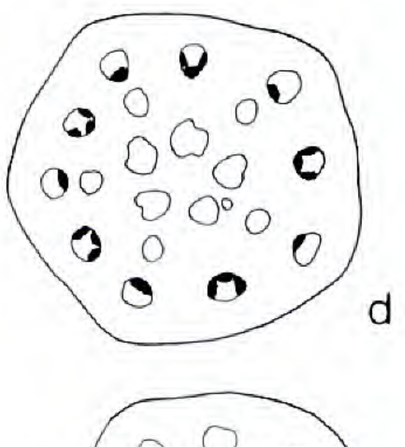


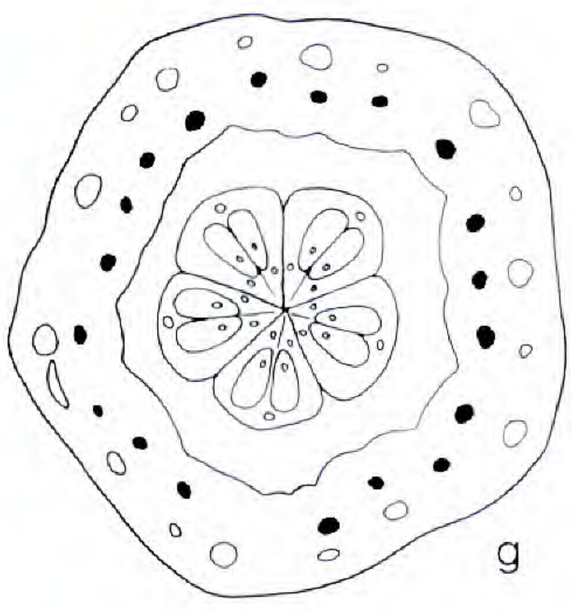


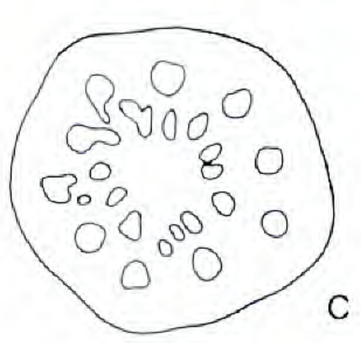


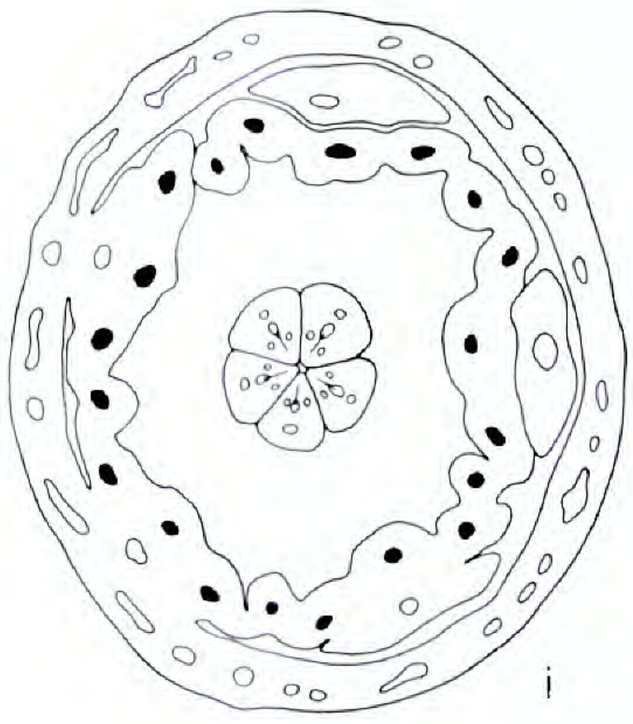


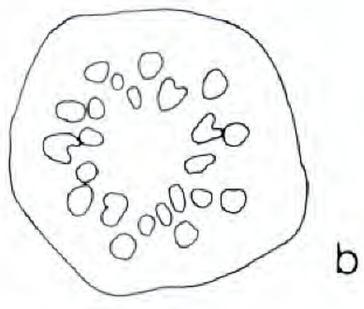


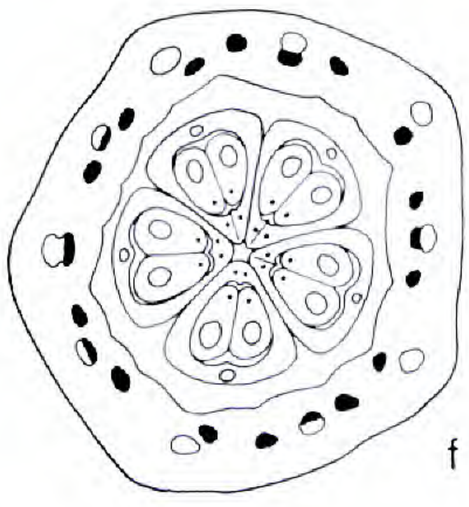












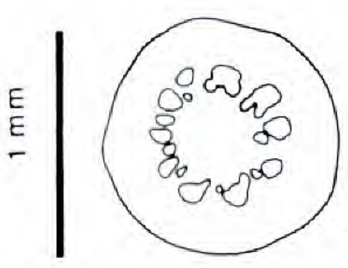


Fig. 6. Vascularization of flowers of *Vauquelinia corymbosa* subsp. *heterodon*. a-j.—Diagrams of vascular system as seen in serial cross sections at levels indicated in fig. k. Stamen traces are indicated by black circles in d-j. Note that mid-sepal traces each give rise to single stamen traces; alternate traces give rise to 2 stamen traces and 1 petal trace before dividing to become marginal sepal traces of 2 adjacent sepals. Note ovary structure. l.—Diagram showing orientation of vascular traces in cleared, flattened hypanthium. Note divergence of stamen, petal traces. m.—Vascular system of sepal as seen from cleared material. Sepals receive 3 traces, one medial, and two marginal. n.—Vascular system of petal as seen from cleared material. Petals receive single traces that branch basally (all from *Henrickson 16076*). Magnifications as indicated, scale in a holds for a-j.

cup (fig. 6c – d). The remaining interior traces organize into five dorsal ovary traces opposite the mid-sepal traces, with the remainder eventually organizing into 10 ventral traces in the center of the receptacle (fig. 6c – d). The peripheral hypanthial traces consist of five mid-sepal traces located in the angles of the pentagonal hypanthium and five marginal sepal-petal traces that in the lower receptacle each have two interior, smaller, marginal traces that eventually fuse completely with these marginal sepal traces. At this level the ovary base is visible as five carpels located opposite the mid-sepal traces each capped with a dorsal trace (fig. 6e). The ovaries are obdeltate with obcordate locules as seen in cross section (fig. 6e) and, at their very base, are completely connate laterally. Slightly above the base the ovaries are separate, and their lateral borders are marked by their contiguous epidermal layers that form distinct double rows of cells (fig. 7b). Similar double rows of cells also line ventral sutures. None of the material examined here showed carpels open along the ventral sutures as reported by Sterling (1966). At a higher level the 5 ovaries are fused along the ventral sutures (fig. 6g – h) and along the inner margins of the carpel sutures; the carpels are usually free along the peripheral portion of the intercarpel suture. This fusion pattern is also evident on the mature fruit (fig. 7c).

Each carpel has a single locule and 2 basal, winged ovules that receive their ovule bundles at the very base of the ovary where the ovule bundles separate from the ventral traces (fig. 5d, 6e). The ventral traces then continue into the ventral portion of the ovary wall as wing bundles. The wing and dorsal traces extend to the top of the ovary and enter into the style (fig. 6h – j).

In the mid to lower hypanthium stamen traces emerge from the 10 peripheral hypanthial traces; first, one each from mid-sepal trace, and at a slightly higher level, a series of three traces develop from each marginal-sepal-petal trace with the two marginal traces separating below the level of the medial stamen traces (fig. 6d – i, l). Each flower then tends to have 20 stamens, occasionally fewer. At the rim of the hypanthium stamens opposite the mid-sepal trace separate first—forming what could be considered the first or innermost series of stamens (fig. 6i), but this is scarcely evident. The other stamens, all derived from the marginal sepal-petal trace, separate from the hypanthium *with* the petals and are briefly adnate to the lower, inner margin of the petals (fig. 6h – i). It is not until after the petals have begun to diverge that the solitary petal traces separate from the marginal sepal traces, entering directly into the base of the petals (fig. 6i) and soon branch into 3 to 5 traces at the petal bases (fig. 6n). Above this point marginal sepal traces give rise to series of horizontal traces in the

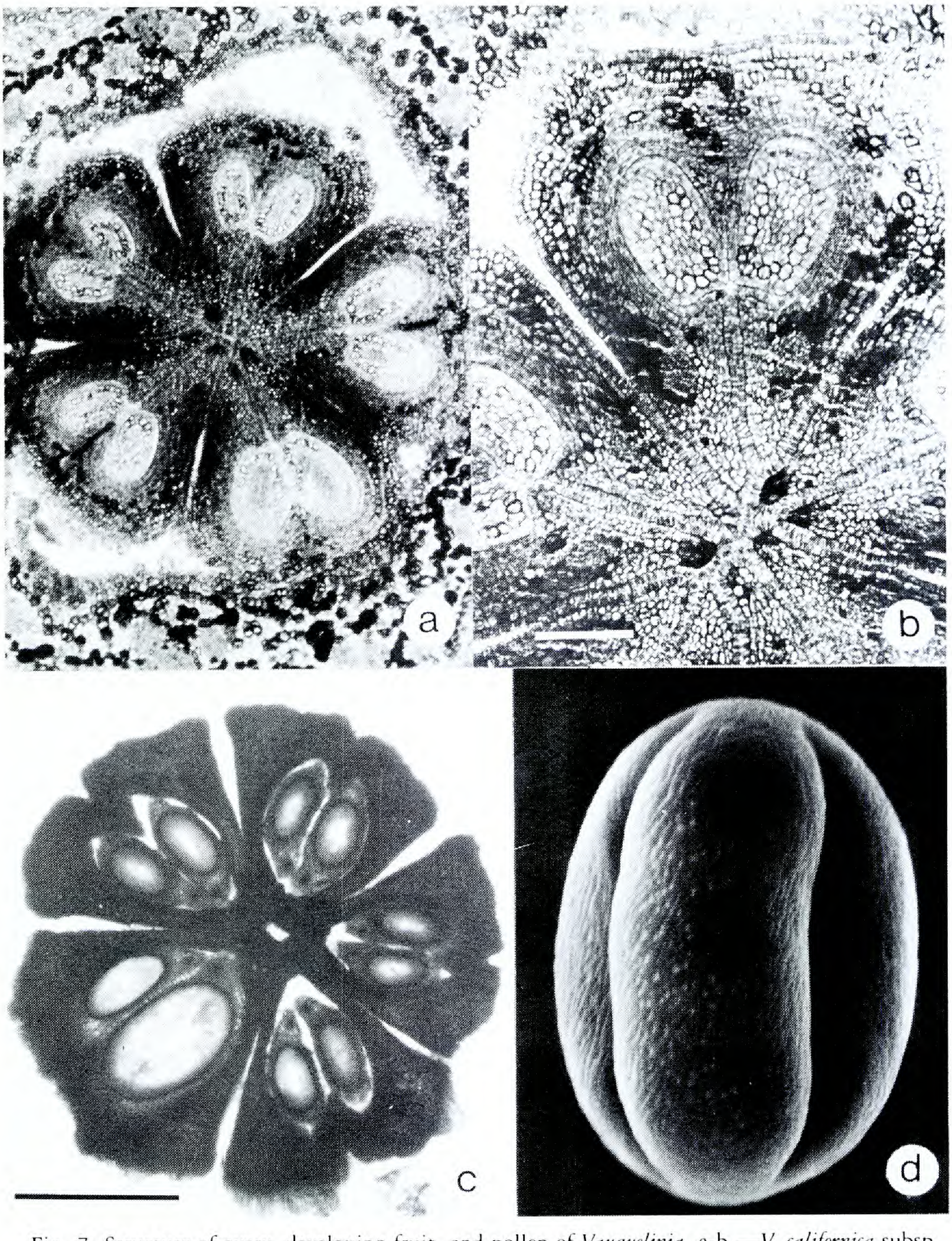


Fig. 7. Structure of ovary, developing fruit, and pollen of *Vauquelinia*. a-b.—*V. californica* subsp. *retherfordii*. a.—Cross section of ovary in young flower. Note carpels are connate centrally but separate along the outer margins. Each carpel has one locule, two ovules. Ovary is ca 0.88 mm in diameter. b.—Expanded view of single carpel showing ovules and two layers of cells forming border between carpels and along ventral suture. Carpel is ca 0.5 mm long. (*Henrickson 15874*). c.—*V. corymbosa* subsp. *corymbosa*. Hand-cut cross section of developing fruit showing 2 ovules per carpel with embryo sacs. Note carpels are connate centrally, separate marginally. (*Hess & Wilhelm 4376*). d.—*V. californica* subsp. *pauciflora*. Dry, non-acetolyzed pollen showing fine striate, finely reticulate sculpturing. (*W. W. Jones 54*). Pollen is ca 16 μm long. Horizontal bars in a-b = 0.1 mm long, in c = 1 mm, in c = 10 μm.

lower sepals and eventually branch, with one branch going to each adjacent sepal (fig. 6l – m).

Sterling (1966) noted that the configuration of the ovary, the fusion along the inner margins, and the paired basal ovules etc., was reminiscent of that found in some Maloideae. But this similarity appears only at the very base of the ovary where carpels are completely fused. Above this point each carpel has a distinct epidermal layer, and although adjacent carpels are contiguous and connivent to one another, they are not fused. Instead there is a distinct double row of epidermal cells, the same as found bordering the ventral suture in both Maloideae and *Vauquelinia*. Sterling (1964) notes that primitive Maloideae have five vascular bundles to each carpel, one dorsal, two wing bundles to the ovary wall, and two separate ovule traces that develop from a central receptacular plexus. With specialization the wing and ovule bundles develop from the basal ventral bundles. The latter situation occurs in *Vauquelinia*. Some Maloideae (*Pyracantha*) have completely separate carpels that are adnate to the hypanthium only at the very base.

Fruits: The ovary matures into a dry, ovoid, woody, capsular fruit (fig. 5f). Each carpel is connate to adjacent carpels near the center but free in the peripheral half (fig. 5f, 7c) and the developing fruit is thus marked with five vertical grooves marking the spaces between the carpels. As the fruit dries and dehisces, the carpels open all along the inner (ventral) suture, across the stylar region, and about half way down along the dorsal trace (fig. 5g). As they dehisce each carpel separates from adjacent carpels. The outer surface of the carpel is strigose, covered with lignified, stiff, erect, unicellular hairs.

Seeds: The two seeds produced in each carpel have basal dicotyledonous embryos, and no endosperm. The seed coat forms a terminal wing whose size and shape conforms to the shape of the locule. At maturity the wings are dry, glabrous, and brownish (fig. 5h).

Embryos: Embryos consist of a basal, terete radicle and two oblong, terminally rounded cotyledons (fig. 5i).

TAXONOMIC TREATMENT

VAUQUELINIA Correa ex Humboldt & Bonpland. Pl. Aequin. 1(6):140. 1807. TYPE: *Vauquelinia corymbosa* Humboldt & Bonpland.

Evergreen, multi-stemmed shrubs to small trees; young stems terete, slender, alternately branched, yellow-green to reddish- or chestnut-brown, tomentulose to villous-canescent with short, tightly crinkled white hairs, tardily to soon glabrate; bark gray to gray-black, smooth or variously fissured, or vertically plaited with age. Leaves alternate to rarely

subopposite-opposite, erect-ascending to spreading, usually variable in size with second and third leaves of a season's increment larger and with different toothing than first- and last-formed leaves; leaf-blades dorsiventral in structure, strongly to slightly coriaceous, usually corneous along margins, plain, or slightly folded along midrib, with margins revolute to variously crisped, linear, lanceolate, oblong-lanceolate, oblong-elliptic, oblanceolate to broadly ovate, acute to rounded, usually mucronate or retuse by terminal dieback at tip, narrowly to broadly, often obliquely cuneate, rounded to subcordate, with margins extending down petiole at base, at margins variously crenulate to serrate, often partially double serrate-crenulate; teeth low, rounded, to ascending-divergent, acute-acuminate, terminating in a caducous gland on inner tip margin, similar caducuous glands often borne in axils of teeth and along margin between teeth and continuing down petiole wings, gland bases persistent, usually darkened; lamina initially tomentulose with tightly crinkled hairs throughout, soon to tardily glabrate, sometimes persistently puberulent along the basal midvein, green, lustrous or dull with midvein impressed above, usually more persistently puberulent-tomentulose, more yellow-green, with venation conspicuous and midvein conspicuously raised beneath, both major and minor veins with bundle sheath extensions; petioles short to elongate, canaliculate, narrowly winged, yellow-green or reddish, puberulent-tomentulose to glabrous; stipules subulate to narrowly deltate, usually dull red-brown, initially tomentulose, glabrescent, glandular-margined, tardily caducous. Flowers borne in terminal, puberulent to tomentulose-villous compound corymbs, these often aggregated at branch tips, with lower branches developing from axils of reduced leaves, upper branches with reduced, linear-subulate, gland-margined, mostly caducous bracts-bracteoles; pedicels bibracteolate; hypanthia obconic to hemispheric, coriaceous, often distinctly veined, initially tomentulose, variously glabrate outside, nectariferous, usually glabrous above a sericeous base, persistent; sepals 5, valvate in bud, green, broadly ovate, more deltate in fruit, erect-spreading, coriaceous, strongly mucronate at tip; margins thin, rounded, often with scattered caducous glands, initially tomentulose-villous, variously glabrate to villous-tomentulose outside, usually persistently villous at least along margins and at tip inside; petals 5, inserted at mouth of hypanthia alternate to sepals, imbricate in bud, white, thickish, oblong-ovate, oblong-obovate, rounded to emarginate at tip, cuneate to rounded, sessile or broadly clawed at base, entire, spreading to reflexed, caducous or reflexed and persistent, tomentulose where exposed in bud, glabrate or floccose at tip; stamens 18 – 20, borne in more or less 1 series on the upper hypanthium; filaments subulate,

connate basally, glabrous, unequal in length and forming generally into 4 size classes with longer filaments slightly broader at base, inflexed in bud, reflexed-spreading in flower; anthers ovoid, bithecal, introrse, longicidal, subversatile with filament attached abaxially, exserted; carpels 5, opposite sepals, basally connate, and borne on a thickened hypanthium-receptacle but free from lateral hypanthium, densely sericeous; ovules 2 per carpel, attached at inside locule base, ascending, anatropous, bitegmic, prolonged apically into a thin, membranous wing; styles 5, erect, glabrous, dilated distally, broadly truncated and stigmatic at tip, yellow, turning dull brown and persisting on fruit. Capsules dark brown, woody, broadly ovoid, sericeous, surrounded by the persisting hypanthium; carpels 5, separating from one another to the base and each dehiscing ventrally to base but dorsally only in the distal half; seeds 2 per locule, compressed, ascending; embryo cotyledons flat, ovate; radicle straight, basal; testa tan to yellow, expanding distally to form a membranous oblong wing longer than the embryo, in outline conforming to locule space; endosperm absent (figs. 8 – 19).

With three species, and ten subspecies, from southern Arizona, southwestern New Mexico, west Texas south to central Baja California, Durango, Tamaulipas, San Luis Potosí, Hidalgo, Querétaro, Puebla, and Oaxaca, México (figs. 9 – 13).

KEY TO SPECIES

A. Leaf blades mostly oblanceolate, oblong-oblanceolate, broadest in the distal half with margins usually distinctly revolute to inrolled, tomentulose beneath at maturity; Puebla and Oaxaca. . . . . 1. *V. australis*

AA. Leaf-blades mostly linear to lanceolate, oblong-lanceolate, ovate or elliptical, broadest in the proximal half or middle with margins flat, crisped or slightly revolute but not inrolled, glabrous to canescent, rarely persistently tomentulose beneath; of northern distribution.

B. Leaf margins crenulate with mostly 2 – 7(– 10) low, rounded teeth per 1 cm; sepal margins without small, sessile glands; plants of northern Baja California, Arizona, to Durango, central Coahuila. . . . . 2. *V. californica*

BB. Leaf margins serrate, serrulate to doubly serrulate, with mostly 1 – 2(– 4) acute to acuminate teeth per 1 cm, when doubly serrate, secondary teeth usually low and rounded; sepal margins mostly with small, sessile, caducous glands; plants of Hidalgo, Querétaro north to San Luis Potosí, Tamaulipas, Nuevo León, eastern Coahuila. . 3. *V. corymbosa*

1. VAUQUELINIA AUSTRALIS Standl. Proc. Biol. Soc. Wash. 31:132. 1918.
TYPE: MÉXICO. PUEBLA: Cerro de Paxtle, vicinity of San Luis Tultitlanapa, Apr 1908, *C.A. Purpus 2729a* (HOLOTYPE: US!; ISOTYPES: F! GH! MO! NY! UC!).

Ovoid, multi-stemmed shrubs to small trees 2 – 8(– 10) m tall; young stems closely, densely, rarely sparsely arachnoid-villous to tomentulose

with slender, tightly crinkled, matted hairs 0.1 − 0.2 mm long, tardily glabrate to glabrate; older stems with smooth gray or gray-brown bark; basal trunks to 2 − 3(− 6) dm in diameter with dark brown, tight, irregularly plaited bark. Leaves ascending; leaf-blades oblanceolate, oblong-oblanceolate, oblong-elliptical, oblong, occasionally narrowly elliptical, usually broadest in distal half, (2 −)3 − 9(− 12.5) cm long, (6 −)10 − 24(− 32) mm wide, [length-width ratio (3 −)3.5 − 5], coriaceous, 0.2 − 0.3 mm thick, obtuse, rounded to acute, mucronate, rarely retuse at tip, narrowly to broadly, often obliquely cuneate with margins continuing down petioles at base, at margins revolute to distinctly inrolled, rarely plain and unevenly crisped, serrulate, serrate or partially doubly serrate with serrations ascending, rarely divergent, blunt or acute, corneous, 0.2 − 1.0(− 2.0) mm long, mostly 3 − 7 per 1 cm, usually tipped with caducous glands 0.1 − 0.2 mm long, sometimes with glands between major serrations; lamina usually initially arachnoid-villous to tomentulose on both surfaces, becoming glabrate, smooth, lustrous, dark green except where more persistently villous to tomentulose along impressed midvein above, more persistently gray-white tomentulose with a close covering of gray-white crinkled hairs except along raised yellow or reddish midvein, sometimes vestiture persisting only along minor venation, occasionally almost glabrate beneath; petioles (4.5 −)7 − 11(− 18) mm long, [(0.2 −)0.12 − 0.09(− 0.07) times as long as leaf blade], yellowish to reddish, adaxially canaliculate, narrowly winged by decurrent leaf margins, mostly with 4 − 7(− 12) pair of caducous glands bordering wings, moderately to sparsely tomentulose adaxially; stipules narrowly deltate, 1 − 2(− 3) mm long, caducous, villous-tomentulose, sometimes glabrate with caducous glands along margins. Compound corymbs 2.5 − 4.5 cm long, 4.5 − 7.5 cm wide, often aggregated at stem tips; lower peduncles 8 − 15(− 20) mm long; pedicels-peduncles sparsely puberulent, villous to tomentulose or tardily glabrate; upper bracts-bracteoles linear to oblong-lanceolate, 1 − 3(− 5) mm long, tomentulose-villous, with glands along margins; hypanthia hemispheric, 1.5 − 2.1 mm long, 2.5 − 3 mm wide, to 5 mm wide in fruit, loosely tomentulose, partially glabrate, greenish outside, sparsely sericeous inside; sepals broadly ovate, 1.3 − 2.5 mm long, to 1.5 − 2.1 mm wide, obtuse, strongly mucronate at tip, at margins thin with 1 − 3(− 4) pair of caducous glands, partially glabrous outside, densely tomentulose particularly along lower margins inside; petals broadly elliptic, obovate to orbicular, (3.2 −)3.4 − 5.2 mm long, (2 −)3.2 − 3.9 mm wide, rounded, rarely emarginate at tip, usually broadly clawed for 0.2 − 0.5 mm or sessile at base, initially villous-tomentulose where exposed in bud but usually

glabrate by anthesis, mostly caducous; filaments 2.6−4.5 mm long; anthers 0.7−0.9 mm long, to 1.3 mm long wet; styles 1−1.4(−2) mm long. Capsules 5.5−6.5 mm long, 4−5 mm wide, sericeous; seeds 4.5−5.5 mm long, 1−1.5 mm wide; mature embryos 2.0−2.5 mm long, 1−1.3 mm wide (figs. 8, 13).

Vauquelinia australis is perhaps the most easily recognized species of the genus, characterized by its oblanceolate, oblong-oblanceolate to oblong, oblong-elliptical, short-petiolate leaves mostly with revolute or distinctly inrolled, closely serrate-serrulate margins (fig. 8). In its typical phase, leaves are persistently, closely, gray-white tomentulose or tomentose along the reticulate minor veins beneath and lustrous, dark green above. Sepal margins bear minute glands, as in most taxa within *V. corymbosa*. However, in its persistent leaf vestiture, short petioles, small teeth and involute margins it appears more similar to *V. californica* than to *V. corymbosa*.

Populations of *V. australis* from near Tehuacán and San Juan Ixcaquixtla, Puebla are distinctive in their tendency to have smaller, more glabrate or nearly glabrous leaves with flatter, non-revolute, often sharply serrate or doubly serrate, more or less crisped margins (fig. 8d−f). Field observations by Hess from the populations near Tehuacán, indicate that these plants occur along a limestone ridge between San Lorenzo and Tehuacán and that the plants appear stunted and heavily grazed. More remote, ungrazed plants had larger, more typically vestitured, undulate or slightly revolute leaf margins characteristic of the species (fig. 8d). Label data of the collection near San Juan Ixcaquixtla also noted heavy grazing pressures. These distinctive specimens could represent heavily grazed plants bearing a juvenile leaf type. Other aspects, however, indicate that the differences exhibited are genetically based. The populations warrant additional study.

Vauquelinia australis is separated from other species of *Vauquelinia* by the trans-volcanic ranges. The importance of the Tertiary-Pleistocene trans-volcanic belt on distribution of plants in México is reviewed by Axelrod (1979).

Vauquelinia australis is known only from three populations in the state of Puebla and three from the state of Oaxaca (fig. 13), where it is locally common on limestone hillsides and canyons from 1670 to 2350 m, primarily in thorn-scrubland or chaparral with species of *Tecoma*, *Karwinskia*, *Ptelea*, *Opuntia*, *Rhus*, *Comarostaphylis*, *Juniperus*, *Lycium*, and *Berberis*. Flowering occurs from April to May.

Representative collections: MÉXICO.

2. VAUQUELINIA CALIFORNICA (Torr.) Sarg.

Rounded to ovoid, obovoid, multi- to single-stemmed shrubs to trees

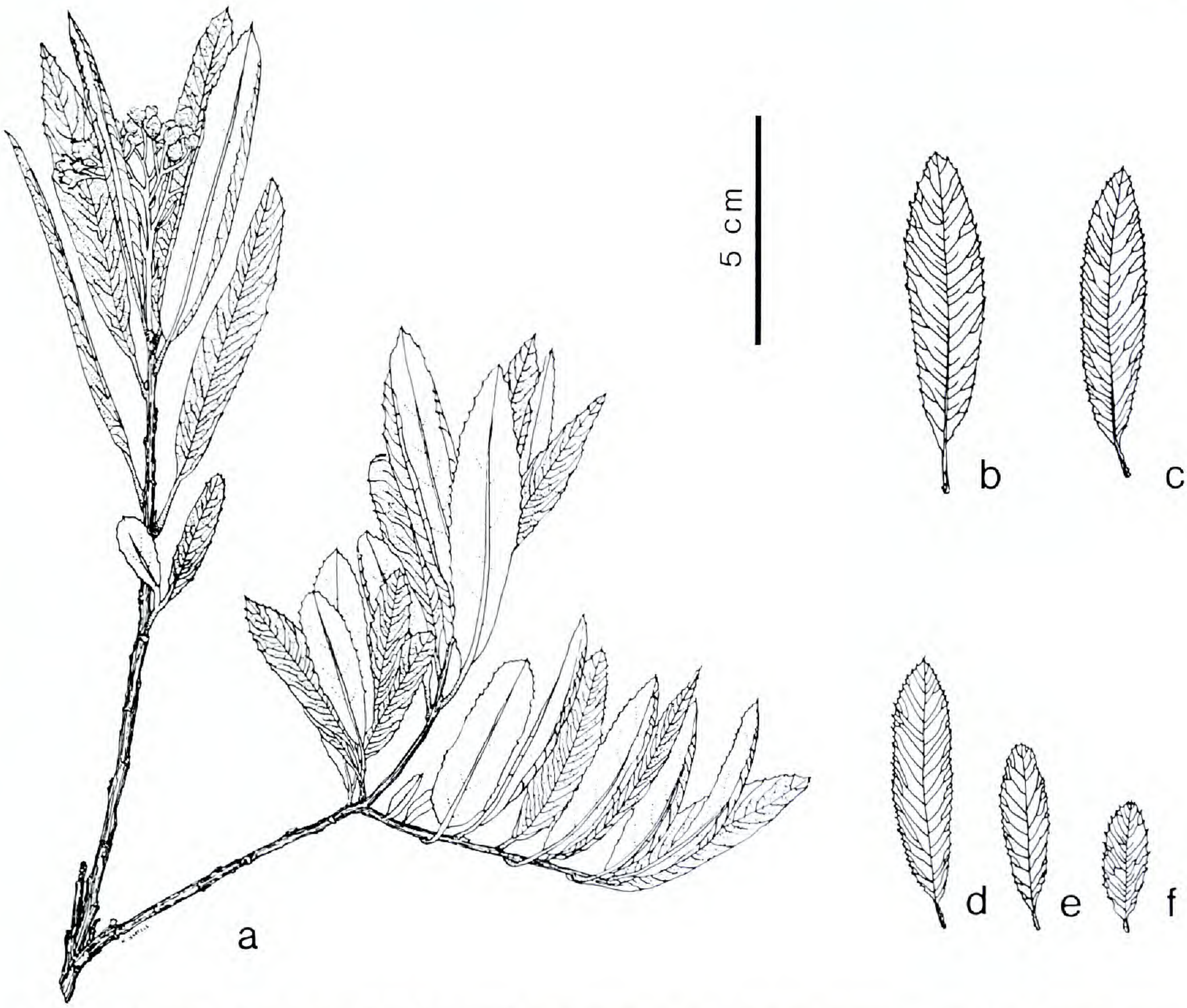


Fig. 8. *Vauquelinia australis*. a.—Young flowering stem showing erect-ascending, bicolored leaves; note recurved margins on some leaves. b-f.—Variation in leaf shape, size. b-d.—Leaves from most populations are broader in distal half (recurved margins are not shown here). *Hess & Wilhelm 4382* from near Nochixtlan, Oaxaca. d-f.—Plants from San Lorenzo near Tehuacan occurring on heavily grazed, limestone hills have much smaller, flat leaf blades. *Hess & Byrne 4671*. Magnifications as indicated in vertical scale.

1 − 6(− 10) m tall; young stems sparsely to closely or densely tomentulose-villous with slender, tightly crinkled, matted hairs 0.1 − 0.3 mm long, tardily glabrate, or persistently tomentulose or canescent with a tight, close covering of coiled hairs; bark smooth, gray to black, developing closely, irregularly plaited on larger trunks. Leaves ascendant to divergent; leaf blades mostly oblong-lanceolate, linear-lanceolate, lanceolate, to variously oblong-elliptical or oblong-ovate, (1.5 −)3.5 − 10(− 15) cm long, (4 −)7 − 15(− 34) mm wide, coriaceous, acute to obtuse, mostly mucronate at tips, abruptly to gradually, often obliquely cuneate to rounded, or subcordate at base, at margins plain, sometimes slightly revolute between serrations, or variously crisped, closely serrulate or crenulate, or partially doubly serrulate or crenulate with 2 − 7(− 10) teeth per cm with serration number depending on development of secondary serra-

tions; serrations ascending to divergent, acute to rounded, 0.1 – 0.5(– 1.5) mm long, gland-tipped, often with additional glands along margins between crenations or serrations, upper serrations margins concave, straight or convex, lower margins concave, straight or sigmoid; lamina often slightly folded along impressed midrib, usually bicolored, initially sparsely to densely, closely villous-tomentulose on both surfaces but this thicker beneath, glabrate or tardily glabrate with persisting, short, crinkled hairs along the impressed midrib or throughout, lustrous or not above, persistently tomentulose to puberulent but vestiture usually much reduced along mid and secondary veins, or nearly to completely glabrate beneath; petioles (1.5 –)4 – 14(– 26) mm long, green-yellow or tinged with red, canaliculate, adaxially winged by decurrent leaf margins, wings usually with glands along margins, variably tomentulose throughout or adaxially; stipules narrowly deltate, 1 – 4 mm long, tomentulose, glabrate, with sessile glands along margins and tips. Compound corymbs small to large, often aggregated at stem tips; pedicels-peduncles densely tomentulose-villous to tomentose, occasionally sparsely pubescent, glabrate; bracts-bracteoles oblong to linear-lanceolate, 1 – 7(– 9) mm long, sparsely to densely tomentulose or puberulent, with sessile glands along margins; hypanthia hemispheric, densely villous-tomentose to sparsely tomentulose, occasionally glabrate, green outside, mostly glabrate-glabrous above a sericeous base inside; sepals thick, broadly ovate, deltate, 1.1 – 2.3 mm long and wide, obtuse to rounded, bluntly mucronate, margins thin, without sessile glands, villous-tomentose to nearly glabrate outside, usually densely villous at least along margins inside; petals oblong-ovate, 2.7 – 5.4 mm long, 2.0 – 3.5 mm wide, rounded to emarginate at tip, broadly cuneate to rounded above a broad claw 0.2 – 0.4 mm long at base, sometime floccose at tip at anthesis but eventually glabrate, recurved and persisting on fruit or not; filaments 2.5 – 5.5 mm long; anthers 0.7 – 1.3 mm long, to 1.8 mm long wet; styles 1 – 2.1 mm long. Mature capsules ovoid, 4.5 – 6.5 mm long, 3.5 – 4.5 mm wide, sericeous; seeds 3.5 – 5 mm long, 0.9 – 1.8 mm wide; embryos 1.6 – 2.7 mm long, 0.8 – 1.2 mm wide.

Vauquelinia californica is distinguished by its oblong-lanceolate to linear, finely crenulate-serrulate-margined, short petiolate leaves, its lack of glands on sepal margins, and its tendency to have marcescent petals. It is here divided into four subspecies ranging from central Arizona southwest to central and southern Baja California, and southwestern New Mexico south to eastern Durango, and eastern and central Coahuila.

KEY TO SUBSPECIES OF *VAUQUELINIA CALIFORNICA*

A. Leaves bicolored, green above, white beneath, (but typically glabrate beneath in central Arizona); Arizona, New Mexico to Baja California, Durango, and central Coahuila.
  B. Leaves lanceolate to oblong-lanceolate or narrowly elliptical, (7)10 − 20(− 32) mm wide, tomentulose, (rarely nearly glabrate beneath, from Maricopa and adjacent Pinal, Gila counties, Arizona), green, lustrous above; central Arizona, and central Baja California. . . . . 2a. *V. californica* subsp. *californica*
  BB. Leaves linear to linear-lanceolate, (4 −)7 − 10(− 13) mm wide, if elliptical then under 4 cm long, persistently white-tomentulose to canescent beneath, slightly puberulent, non-lustrous above.
    C. Leaf-blades (3.5 −)5 − 11(− 14) cm long, (6 −)7 − 12(− 14) mm wide; petioles (4 −)6 − 13(− 22) mm long; leaves permanently white-tomentulose beneath; southwestern Arizona (Ajo Mountains) and northern Baja California .2b. *V. californica* subsp. *sonorensis*
    CC. Leaf-blades (1.5 −)2.0 − 5.5(− 7.7) cm long, 4 − 9(− 13) mm wide; petioles (2 −)4 − 9(− 11) mm long; leaves closely canescent beneath; extreme southwestern Coahuila and northeastern Durango. . . . . 2c. *V. californica* subsp. *retherfordii*
AA. Leaves glabrate, green or yellow-green on both surfaces, occasionally with few trichomes along midvein; extreme southwestern New Mexico, adjacent southeastern Arizona, south to eastern Chihuahua, Durango, and also central Coahuila. . . . . 2d. *V. californica* subsp. *pauciflora*

2a. VAUQUELINIA CALIFORNICA (Torr.) Sarg. subsp. CALIFORNICA Gard. & Forest 2:400. 1889. *Spiraea californica* Torr. in Emory, Notes Mil. Recon. 140. 1848. TYPE: ARIZONA. Gila Co.: high mountains near the Gila, Nov 1846, *Major W. Emory s.n.* (HOLOTYPE: NY!).

Vauquelinia corymbosa Torr. in Emory, Rep. U.S. & Mex. Bound. 2:64. 1859 *non* Humb. & Bonpl.

Vauquelinia torreyi S. Wats. Proc. Amer. Acad. Arts 11:147. 1876.

Multi-stemmed, straggly shrubs to small rounded, obovoid trees 1.2 − 5(− 8) m tall; young stems initially closely tomentulose with tightly crinkled hairs 0.1 − 0.2 mm long, usually persistently canescent with coiled hairs or tardily glabrate. Leaf blades oblong-lanceolate, lanceolate, linear-lanceolate, occasionally oblong-elliptical to oblong-ovate, rarely oblanceolate, (3.5 −)4 − 9(− 15) cm long, (7 −)10 − 20(− 34) mm wide, [leaf-blade length-width ratio (2 −)3 − 6(− 7.4)], coriaceous, 0.23 − 0.27 mm thick, weakly to strongly bicolored, acute, obtuse, mucronate or retuse by dieback at tip, abruptly to gradually, often obliquely cuneate to rounded, truncate, or when very broad, subcordate at base, at margins uniformly, closely crenulate or serrulate or partially doubly crenulate-serrulate with (2 −)3 − 7(− 10) gland-tipped teeth per 1 cm, teeth usually small, rounded, 0.1 − 0.4 mm long, sometimes more serru-

late, with acuminate, divergent to ascending serrations 0.5 – 1.4 mm long, often with additional glands in axils of teeth and along margins between teeth; lamina often slightly folded along midrib, green, yellow-green, with yellow mid and secondary veins, initially villous-tomentulose, mostly glabrate or glabrous, lustrous, except where persistently puberulent along depressed midrib above; usually whitish with a more persistent puberulence of lightly coiled hairs, these sometimes diminishing along secondary veins and along the more glabrate midvein, sometimes nearly glabrescent beneath; petioles (4 –)7 – 15(– 26) mm long, [(0.8 –)0.12 – 0.2(– 0.25) times as long as leaf blades], puberulent-tomentulose with curled hairs throughout or only adaxially, wings broad or very narrow with 2 – 12 pairs of often conspicuous, sessile glands. Compound corymbs 3 – 5(– 12) cm long, 3 – 8(– 13) cm wide; lower peduncles 11 – 65 mm long; pedicels-peduncles puberulent-tomentulose, tardily glabrate; upper bracts-bracteoles lance-subulate, 1 – 5(– 7) mm long, villous-tomentulose with glands along margins; hypanthia 2 – 2.5(– 3) mm long, 2 – 3.7 mm wide, to 4.5 mm wide in fruit, tomentulose-villous, tardily glabrate outside, glabrous below stamens inside; sepals 1.4 – 2.1 mm long, 1.5 – 2.3 mm wide, mucronate, margins thin, lacking sessile glands, puberulent-villous outside, villous particularly along margins inside; petals oblong-obovate, oblong-ovate, 4 – 5 mm long, 2.5 – 3.5 mm wide, often floccose at tip but glabrate, recurving and persisting around fruit; filaments 3 – 5.5 mm long; anthers 0.8 – 1.1 mm long, to 1.5 mm long wet; styles 1.7 – 2 mm long. Capsules 5 – 6.5 mm long, 3.5 – 4.5 mm wide; seeds 4 – 5 mm long, 1.2 – 1.3 mm wide; embryos 2.1 – 2.6 mm long. $n = 15$ (Goldblatt 1976). (figs 1a-b, 9, 10).

Vauquelinia californica subsp. *californica* is characterized by its relatively large, oblong-lanceolate, lanceolate to linear-lanceolate, closely crenulate to doubly crenulate, short-petiolate leaves with leaf blades mostly 4 – 9(– 15) cm long, (7 –)10 – 20(– 34) mm wide, with (2 –)3 – 7 (– 10) teeth per 1 cm margin (fig. 10). In most collections leaves are distinctly bicolored, glabrate or weakly puberulent, at least along the midveins above, and variously, persistently, closely tomentulose to canescent beneath with a vestiture of tightly coiled hairs.

In populations from the Superstition Mountains in northwestern Pinal County, north through the Apache Trail, Fish Creek area in adjacent Maricopa County, and in the Pinal and Mescal Mountains in southern Gila County, leaf blades tend to lose more vestiture on the lower surface, becoming glabrate, or nearly so, except along the midveins. In this character they approach *V. californica* subsp. *pauciflora* that occurs in extreme southeastern Arizona and adjacent New Mexico south into eastern Durango, and central

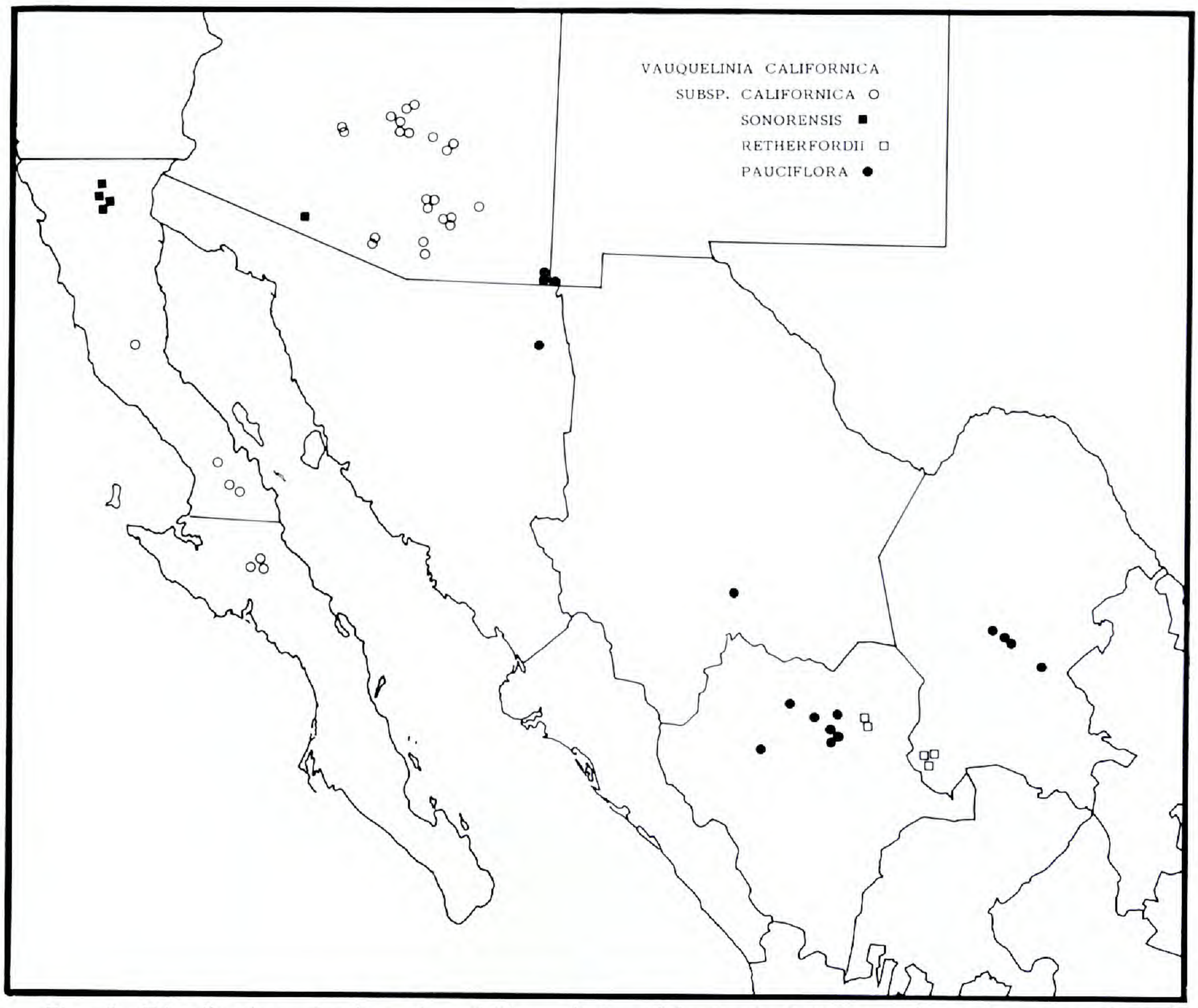


Fig. 9. Distribution of subspecies of *Vauquelinia californica* in México and southwestern United States.

Coahuila. In leaf size, however, they compare more with other populations of *V. c.* subsp. *californica*. Not all specimens are completely glabrate on the lower leaf surface, but retain some vestiture. Thoughts of nomenclaturally recognizing these more glabrate populations were rejected as there appears to be no sharp separation in this vestiture character. Populations from central Baja California, in contrast, tend to have more strongly and persistently vestitured lower leaf surfaces.

The isolated populations of *V. c.* subsp. *californica* exhibit considerable inter- and intra-populational variation. Williams (1971) made statistical analyses of various leaf features of five Arizona populations of *V. c.* subsp. *californica* from the Baboquivari Mountains (Pima County), the Santa Catalina Mountains (Pima County), two areas in the Mescal Mountains (Gila and Pinal counties), and the Superstition Mountains (Pinal County). He found that each population varied in relative leaf length, width, petiole length and, marginal toothing, with populations from the Molino Canyon in the Santa Catalina Mountains averaging the shortest leaves and shortest

petioles (fig. 10e – f), those in Baboquivari Canyon (fig. 1 – n) usually having the narrowest leaves and the least number of marginal teeth per 1 cm, but the differences were not statistically significant. In fig. 10 we show a sample of the wide variation of leaf outline inherent in this taxon, both between and within populations.

Differences also occur in the amount of vestiture retained on stems and inflorescences, in the density and development of marginal leaf toothing (i.e., whether closely or coarsely toothed), and the development of marginal glands. Floral features also undoubtedly vary between populations, but, as flowering material is not available from all populations, these characteristics could not be completely analyzed. Such strong variation is perhaps expected in a taxon whose present interpluvial distribution consists of a series of relictual populations occupying mesic microhabitats in highly isolated ranges.

The type specimen of *V. californica* was apparently collected near the Mescal Mountains in Gila County, Arizona. Emory (1848) noted that during November of 1846, he was "following the course of the Gila River, occasionally forced into the mountains to avoid the canyons." The map accompanying the text indicates that he was at that time on the north side of the river, quite possibly in the Mescal Mountains. There are no other collections known to us from Gila County, Arizona. Williams (1971) studied a population from that general area, only on the south side of the Gila River. He concluded that his collections from the Mescal Mountains were similar to those of Emory's type collection.

Vauquelinia californica subsp. *californica* is locally common in canyons and hillsides, often in rock crevices in both limestone and granite substrates in shrubland communities of the upper Sonoran Desert from just above the desert plains to the lower pinyon-juniper zones (Williams 1971). Populations are known from the Mazatal, Superstition, Pinal, Mescal, Sierra Estrella, Santa Catalina, Rincon, Baboquivari, Santa Rita mountains, and Teran Hills in Maricopa, Gila, Pima, and Cochise counties of south central Arizona, and in the Sierra San Borja, Sierra San Francisco and other scattered ranges of central Baja California, México at elevations from 700 to 1800 m (fig. 9). It occurs in association with a large number of species including *Acacia greggii*, *Agave palmeri*, *A. schottii*, *Aloysia wrightii*, *Artemisia ludoviciana*, *Ayenia pusilla*, *Calliandra humilis*, *Carnegiea gigantea*, *Crossosoma bigelovii*, *Dasylirion wheeleri*, *Dalea formosa*, *Dodonaea viscosa*, *Eriogonum wrightii*, *Erythrina flabelliformis*, *Fouquieria splendens*, *Gutierrezia microcephala*, *Haplopappus laurifolius*, *Krameria parvifolia*, *Opuntia acanthocarpa*, *Opuntia phaeacantha*, *Quercus spp.*, *Porophyllum gracile*, *Simmondsia chinensis*, *Yucca spp.* and species of *Andropogon*, *Aristida*, *Bouteloua*,

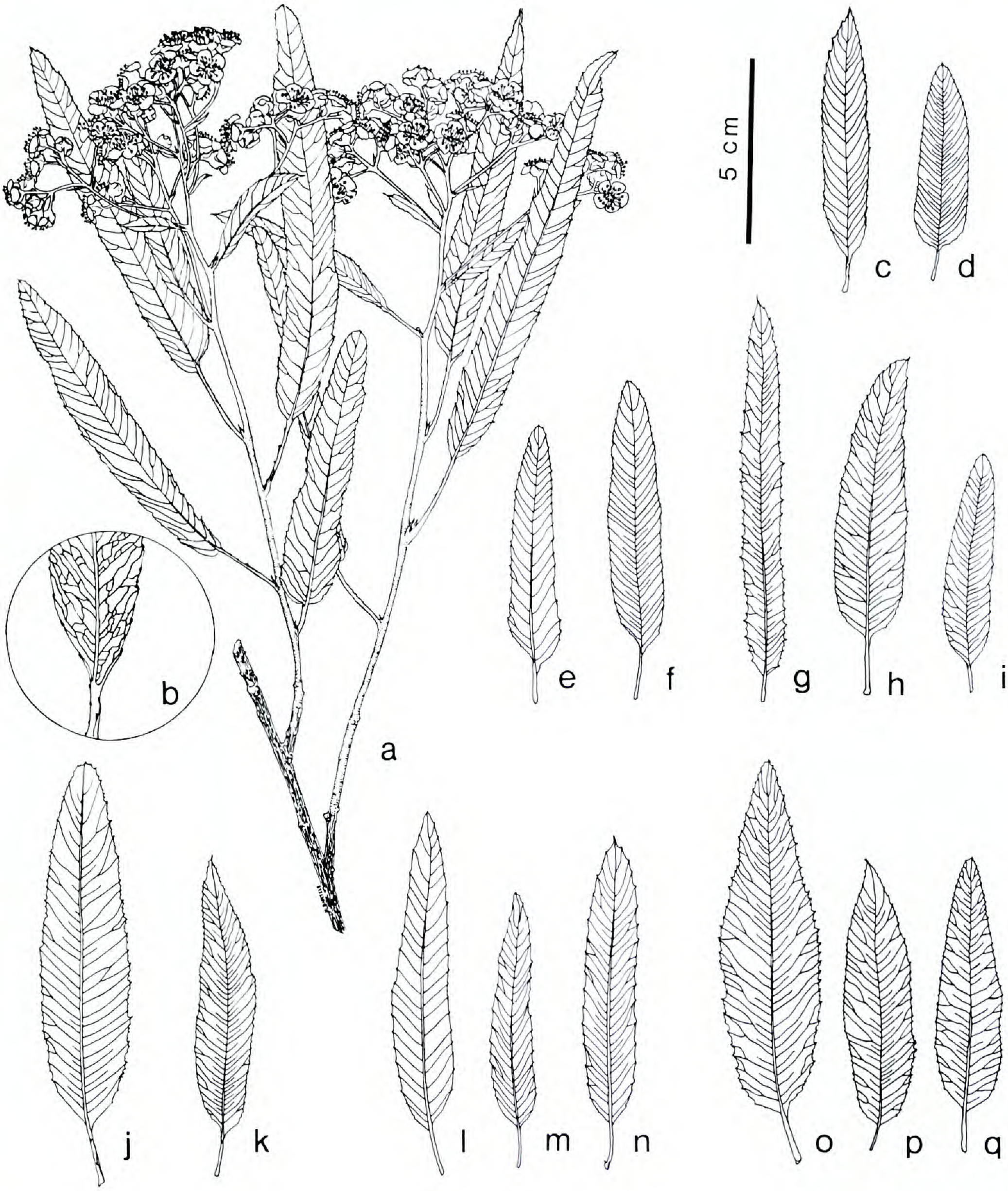


Fig. 10. *Vauquelinia californica* subsp. *californica*. a.—Flowering young stem showing erect-ascending leaves. Note reduced leaves subtending basal peduncles in inflorescences. b.—Leaf base showing glands on petiole wings and continuing up leaf margins. c-q.—Leaf-shape, petiole-length variation throughout range. c-d.—Leaves from Rincon Mountains, SE of Tucson, Pima County, Arizona. c.—*Blumer 3611*. d.—*B. Maguire 11702*. e-i.—Leaves from Santa Catalina Mountains, NE of Tucson, Pima County, Arizona. f.—*M.E. Jones s.n.*. g.—*Thornber 228a*. g-i.—Variation in a single population collection. *Hess & Wilhelm 4256*. j-k.—Variation in leaves from Apache Gap area, E of Phoenix, Maricopa County, Arizona. Both *Hess & Wilhelm 4251*. l-n.—Leaves from Baboquivari Mountains, Pima County, Arizona tend to be narrower, approaching those from the Ajo Mountains. l-m.—*Gilman 127*. n.—*M.E. Jones 24781*. o-q.—Leaves from Sierra Borja in Baja California, México. o.—*Moran 8085*. p.—*Moran 11529*. q.—*Moran 11720*. Magnifications as indicated.

Eragrostis, *Heteropogon*, *Lycurus*, *Muhlenbergia*, *Panicum*, *Tridens*, *Cheilanthes*, *Notholaena*, *Pellaea*, *Selaginella*, *Arabis*, *Echinocereus*, *Euphorbia*, and, *Galium* etc. (Williams 1971).

Representative collections: U.S.A.: Arizona. **Cochise Co.**: S end Teran Hills, at pass W of Allen Flat, road from Cascabel to Willcox T14S R21E S22, 3 Jan 1983, *Yatskievych & Windham 83-18* (ARIZ). **Gila Co.**: Devils Canyon, Pinal Mts., 11 Jul 1926, *Peebles, Harrison & Kearney 2316* (ARIZ); 2 mi E of Coolidge Dam, 2 Jun 1943, *Darrow s.n.* (ARIZ); Mescal Mts., 19 Jul 1976, *Bingham 2366* (ASU). **Maricopa Co.**: Fish Creek, Apache Trail, 21 May 1929, *Eastwood 17386* (CAS, DS-2 sheets, F-3 sheets, NY-2 sheets, US); Near Canyon Lake, Salt River, 21 Jun 1928, *Peebles & Harrison 5538* (ARIZ, US); Apache Trail, 1 mi N of Apache Gap, 3 Jan 1932, *Gillespie 8731* (DS, GH, NY, POM, UC, US). *Pima Co.*: Santa Catalina Mts., Jun 1882, *Pringle s.n.* (A-2 sheets, F-3 sheets, NY-3 sheets, US); Summit, Santa Catalina Mts., Apr 1881, *Lemmon 155* (GH); Sabino Canyon, Santa Catalina Mts., 7 Oct 1894, *Toumey s.n.* (A, NY-2 sheets, US); Manning Trail, Rincon Mts., 11 Apr 1909, *Blumer 3611* (ARIZ, DS, UC); Near Colossal Caves, Rincon Mts., 20 Mar 1930, *McKelvey 516* (GH); Pantano, Mar 1881, *Vasey s.n.* (F, NY, US); Baboquivari Canyon, Baboquivari Mts., 23 Sep 1931, *Gilman 127* (A, ARIZ, DS, GH, NY). **Pinal Co.**: Superstition Mts., 16 Feb 1930, *Fulton & Hastings 6387* (CAS, NY, POM, US); Superior, along stream, 9 Jun 1935, *Whitehead 1354* (US); Sierra Estrella Regional Park, N-facing canyon of Squaw Tit, 20 Oct 1974, *McGill, Franklin, E. & M. Sundell S680* (ASU, RSA).

MÉXICO. **Baja California Norte**: Cliff on S rim of canyon, El Metate 30°11′N, 115°08′W, 29 Dec 1963, *Moran 11447* (DS, SD, UC); Sierra de Borja, upper slope of Cerro el Sauco, 28°46′N, 113°39′W, 27 Mar 1960, *Moran 8085* (DS, SD, UC); N slope of summit of Cerro la Chona, 28°24′N, 113°35′W, 19 Mar 1966, *Moran 12789* (DS, SD); Summit, Cerro la Sandía, 28°24′N, 113°27.5′W, 24 Jan 1964, *Moran 11529* (DS, MEXU, SD, UC). **Baja California Sur**: Sierra San Francisco, summit of Cerro Natividad, 27°28′N, 113°05′W, 24 Feb 1964, *Moran 11748* (DS, LL, SD, UC); Sierra San Francisco, Cerro la Laguna, 27°35′N, 113°02′W, 24 Nov 1976, *Moran 23844* (ARIZ, CAS, SD); Sierra San Francisco, summit of Cerro de la Higuera, 27°31′N, 113°00′W, 21 Feb 1964, *Moran 11720* (ARIZ, DS, RSA, SD, UC, US). **Sonora**: Sierra Verde (probably Baboquivari Mts., Pima Co., Arizona), 17 Jul 1855, *Schott s.n.* (F, GH, MO, NY-2 sheets).

2b. Vauquelinia californica subsp. **sonorensis** Hess & Henrickson subsp. nov.

A ssp. *californica* et *pauciflora* foliis linearibus vel lineari-lanceolatis, infra dense albis, tomentosis et a subsp. *retherfordii* laminis 6 − 12(− 12.5) cm longis, et petiolo 6 − 16(− 22) mm longo differt.

Multi-stemmed shrubs to small trees 1 − 4(− 7) m tall; young stems initially densely white-tomentulose with tightly crinkled hairs 0.1 − 0.2(− 0.3) mm long, vestiture persisting though diminishing in stature, becoming more canescent. Leaf blades linear, narrowly oblong to oblong-lanceolate, (2.5 −)5 − 11(− 15) cm long, (5 −)7 − 12(− 17) mm wide, [length-width ratio (5.5 −)7 − 13(− 15)]; coriaceous, 0.26 − 0.3 mm thick, strongly bicolorous, acute to obtuse, occasionally retuse,

acuminately mucronate at tip, abruptly to gradually, usually obliquely cuneate to nearly rounded at base, at margins thickened, very slightly revolute between teeth, sometimes crisped, uniformly and closely crenulate to serrulate, occasionally partially doubly crenulate with 2 − 3(−6) gland-tipped teeth per 1 cm, crenulations usually low, rounded, (0.1 −)0.2 − 0.4 mm long, sometimes barely evident, or margins more serrulate with acuminate, divergent to ascending teeth 0.6 − 2.5 mm long, often some leaf-blades completely entire; lamina initially villous-tomentulose but soon or tardily glabrate, often with a residual close vestiture of coiled hairs along midrib, generally dull, not lustrous above, persistently white villous-tomentulose with curled hairs forming a layer 0.1 − 0.15 mm thick, though this sometimes diminishing in older leaves, often less densely vestitured along secondary veins with vestiture much reduced along raised yellow midvein beneath; petioles (4 −)6 − 16(−22) mm long, [(0.05 −)0.07 − 0.14(−0.25) times as long as leaf blade], strongly villous-tomentulose throughout or adaxially, 0.8 − 1.2 mm thick, wings thick or thin, with 4 − 6 pair of sessile caducous glands. Compound corymbs 1.5 − 4.5 cm long, 2 − 6.5 cm wide, often clustered at branch tips, rather divergently branched; basal peduncles 11 − 20 mm long; pedicels-peduncles villous to tomentulose with crinkled hairs 0.2 − 0.5 mm long; upper bracts-bracteoles 1 − 5(−9) mm long with glandular margins, densely white villous-tomentose; hypanthia 2 − 2.5 mm long, 3 − 3.5 mm wide, to 4.5 mm wide in fruit, strongly white-villous-tomentulose outside, glabrous inside except at base; sepals 1.3 − 1.8 mm long. 1.6 − 2 mm wide, with yellow, gland-like mucro at tip, margins thin, eglandular, villous-tomentulose outside, generally glabrous except at tip and base inside; petals oblong-ovate, 4 − 5 mm long, 2.4 − 3 mm wide, floccose where exposed in bud, glabrate; filaments 3 − 5 mm long; anthers 1.1 − 1.3 mm long, to 1.8 mm long wet; styles 1.8 − 2.0 mm long. Capsules 5 − 6 mm long, 3.5 − 4 mm wide; seeds 3.5 − 4 mm long, 0.9 − 1.2 mm wide; embryos not seen.

TYPE: ARIZONA. Pima Co.: Organ Pipe National Monument, Arch Canyon, 22 mi s of Why and 12 mi e of visitor center in Ajo Mountains, 31°57′N lat, 112°40′W long, 850 m, 2 Jun 1978, *Hess & Wilhelm 4259* [HOLOTYPE: MOR!; ISOTYPES: (to be distributed)]. (figs. 9, 11a − c).

Vauquelinia californica subsp. *sonorensis* is characterized by its narrow, linear to linear-lanceolate, strongly bicolored leaves with persistently tomentulose lower leaf surfaces, young stems, inflorescences, and hypanthia-calyces (fig. 11a − c).

Subspecies *sonorensis* is restricted to the Ajo Mountains in Pima County, Arizona (in Alamo, Grass, and Arch canyons) and in local areas on the

eastern slopes of the Sierra Juarez in northern Baja California, México (fig. 9). Though separated by some 250 km, the two populations are very similar in most characteristics, though populations in the Sierra Juarez have slightly longer and narrower leaf blades and slightly longer petioles. The populations of *V. c.* subsp. *californica* from central Baja California also have more strongly bicolored leaves, and more densely vestitured stems, inflorescences, etc. than those from Arizona, but the vestiture is not as dense or thick as in subsp. *sonorensis* and the leaves are more lanceolate to oblong-lanceolate, as in other populations of subsp. *californica* in Arizona. Some plants from the adjacent Baboquivari Mountains in Pima County, Arizona have narrow leaves somewhat similar to those of subsp. *sonorensis*, but the plants lack the characteristic dense vestiture on stems, inflorescences, and lower leaf surfaces.

Subspecies *sonorensis* occurs in rhyolite and andesite canyon margins and hillsides, often near ephemeral drainages from 750 – 1500 m, in Arizona with *Simmondsia chinensis, Agave desertii, Aloysia wrightii, Artemisia ludoviciana, Celtis reticulata, Dodonaea viscosa, Eriogonum fasciculatum, E. wrightii, Fouquieria splendens, Gutierrezia microcephalum, Haplopappus laricifolius, Janusia gracilis, Juniperus monosperma, Opuntia phaeacantha, Quercus ajoensis, Sapindus saponaria*, and species of *Aristida, Bouteloua, Muhlenbergia, Stipa, Tridens, Cheilanthes, Notholaena, Pellaea*, and *Selaginella*, and in Baja California in the ecotone between the Sonoran Desert woodland the pinyon wooodlands with *Agave desertii, Brickellia arguta, Eriogonum fasciculatum, Haplopappus cuneatus, Keckiella antirrhinoides, Pinus quadrifolia, Quercus turbinella*, and species of *Berberis, Opuntia, Echinocereus, Stipa, Arabis, and Ferocactus*.

Representative collections: U.S.A.: ARIZONA. **Pima Co.**: Canyons of Ajo Mts., 2 Apr 1944; *Clark 11575* (GH, TEX); Ajo Mountains, Organ Pipe Cactus National Monument, main fork of Alamo Canyon, 15 Aug 1952, *Tucker 2427* (CAS, UC); Ajo Mountains, Alamo Canyon, 19 Apr 1942, *Cooper 597* (ARIZ, ASU); Summit of Bull Pasture Trail, Organ Pipe National Monument, 11 Oct 1976, *Cummins s.n.* (ARIZ).

MÉXICO: **Baja California Norte**: 18 rd mi SSE of La Rumarosa near Rancho San Ignacio (La Milla) in canyon N of Cerro la Milla, 27 Jul 1985, *Henrickson 20281* (TEX); El Torundo, 32°25′N, 115°53′W, 16 Mar 1968, *Moran 14825* (SD); Head of Cantilles Canyon, 32°18′N, 115°55′W, 3 Apr 1966, *Beauchamp s.n.* (SD); E side of Sierra Juarez, Tajo Cañon, 32°16′N, 115°55′W, 9 Sep 1957, *Moran 6105* (DS, RSA, SD); Sierra Juarez, Casimiro, NE of El Topo, 32°18′N, 115°54′W, 27 Sep 1970, *Moran 18190* (SD, DS, RSA).

2c. VAUQUELINIA CALIFORNICA subsp. **retherfordii** (I.M. Johnston) Hess & Henrickson, stat. et comb. nov. *Vauquelinia retherfordii* I.M. Johnston. J. Arnold Arbor. 24:234. 1943. TYPE: México. COAHUILA: Sierra Jimulco, 11 km ne of Jimulco, 28 Jun 1941, *L.R. Stanford, K.L. Retherford, & R.D. Northcraft 87* (HOLOTYPE: GH!; ISOTYPES: ARIZ! DS! MO! NY! UC!).

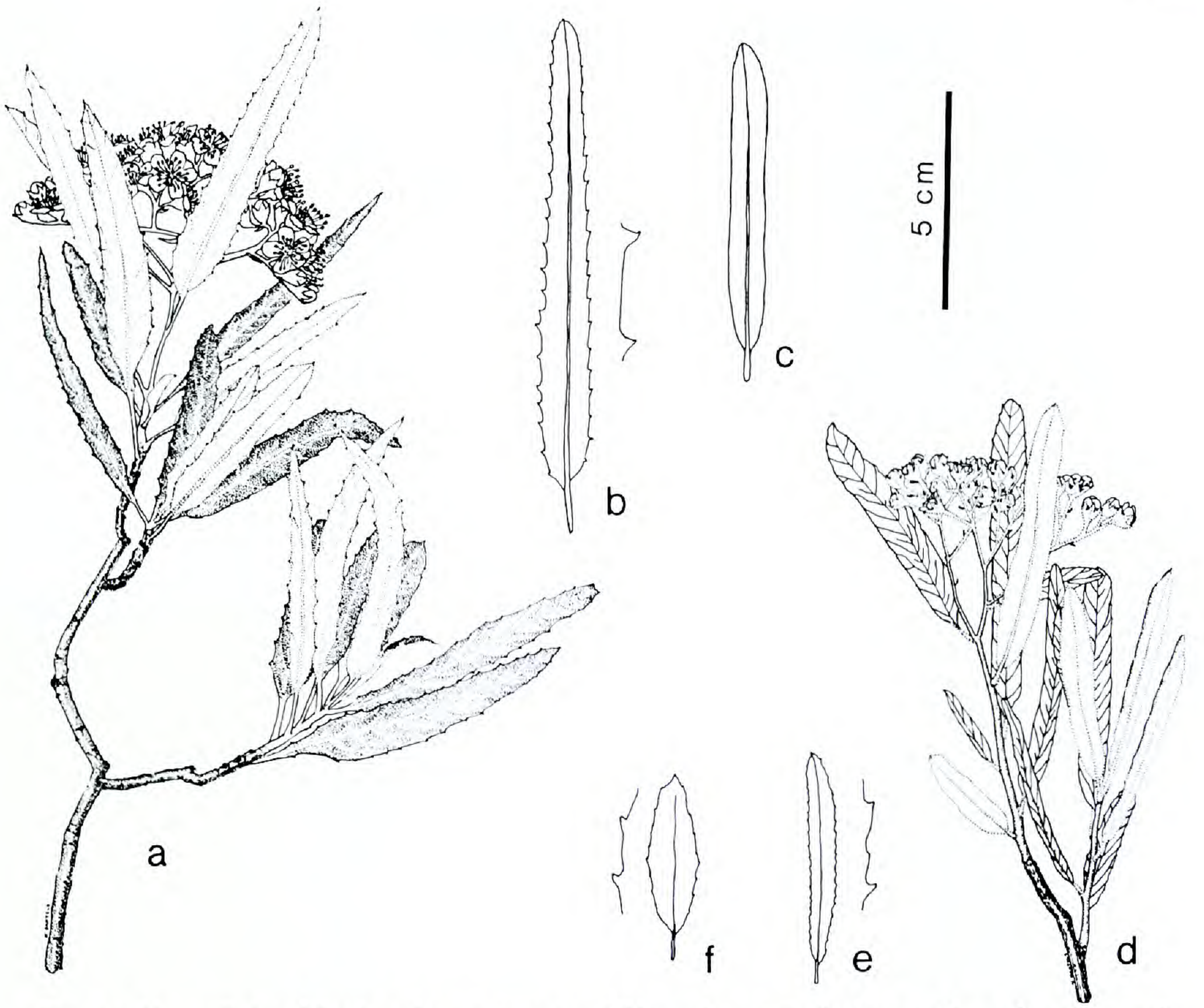


Fig. 11. *Vauquelinia californica* subsp. *sonorensis* and *V. c.* subsp. *retherfordii*. a-c. *V. c.* subsp. *sonorensis*. All collections from the Ajo Mountains, Pima County, Arizona. a.—Young stem showing characteristic oblong-lanceolate, bicolored leaves and flowers. *Hess & Wilhelm 4259*. b.—Leaf outline showing coarse toothing (toothing expanded in outline at right). *Harbison 45544*. c.—Occasional plants have some entire leaves. *Hess & Wilhelm 4259*. d-f.—*V. c.* subsp. *retherfordii*. d.—Young stem showing narrow oblong, bicolored leaves, flowers. Collection from the Sierra de Jimulco, Coahuila, México. *M.C. Johnston et al. 11492*. e-f.—Leaf outlines with marginal toothing expanded. e.—From type specimen from Sierra Jimulco, Coahuila, México. *Stanford et al. 87*. f.—An abnormal narrowly ovate leaf from collection in Sierra Rosario in Durango, México. *Wendt et al. 10021*. Magnifications as indicated, vertical bar = 1 cm for leaf margin enlargements.

Multi-stemmed shrubs to ovoid small trees $2-4(-6)$ m tall; young stems closely, usually persistently canescent with tightly coiled, white hairs $0.1(-0.2)$ mm long, with vestiture usually not completely covering stems, tardily glabrate. Leaf blades linear-lanceolate, narrowly oblong, oblong-elliptical, in one collection, broadly oblong-ovate, $(1.5-)2-5.5(-7.7)$ cm long, $4-9(-15)$ mm wide, [length-width ratio $(2-)5-9$], slightly coriaceous, $0.22-0.27$ mm thick, obtuse to acute, mucronate at tip, abruptly to gradually, usually obliquely cuneate at base, at margins usually somewhat revolute or variously coarsely crisped, closely crenulate-serrulate or partially doubly crenulate with $3-5(-8)$ gland-

tipped teeth per 1 cm, teeth usually low, rounded, (0.1 −)0.2 − 0.4 mm long, sometimes scarcely evident, rarely absent in some leaves, occasionally serrulate or distally serrulate with ascending, acute, teeth 1.0 − 1.2 mm long, sometimes with glands in axils of teeth or on margins between teeth; lamina green, not lustrous, initially sparsely, closely puberulent with coiled hairs, usually glabrate with a yellow, sunken midrib above, grayish, persistently very closely canescent except along raised yellow or basally reddish midrib beneath; petioles (2 −)4 − 9(− 11) mm long, [(0.05 −)0.1 − 0.2(− 0.25) times as long as leaf-blade] sparsely to densely canescent throughout, 0.8 − 1.1 mm thick, wings narrow or tapering, sometimes with few caducous glands along margins. Compound corymbs 1.2 − 5 cm long, 1.5 − 7 cm wide, often aggregated; basal peduncles 4 − 18 mm long; pedicels-peduncles canescent to tightly tomentulose with hairs to 0.1 − 0.2 mm long, very tardily glabrate; upper bracts-bracteoles subulate, 0.7 − 2.2 mm long, marginal glands not evident; hypanthia 1.7 − 2.2 mm long, 2.5 − 3.0 mm wide, to 3.8 mm wide in fruit, puberulent with coiled hairs outside, sericeous to partially glabrous inside; sepals 1.1 − 1.9 mm long, 1.4 − 1.8(− 2.2) mm wide, mucronate, at margins thin, without glands, puberulent outside, sericeous to partially glabrous, densely villous along margins inside; petals oblong-obovate, oblong-ovate, 2.7 − 4.4 mm long. 2 − 2.7(− 3.2) mm wide; filaments 2.7 − 5.0 mm long, anthers 0.7 − 0.9 mm long, to 1.2 mm long wet; styles 1.8 − 2.0 mm long. Capsules 5 − 6.5 mm long, 3.5 − 4.5 mm wide; seeds 4 − 5 mm long, to 1.3 − 1.8 mm wide; embryos 2 − 2.2 mm long, 1.1 mm wide (fig. 11d − f).

Vauquelinia californica subsp. *retherfordii* is characterized by its generally small, narrow, bicolored leaves that are dull, not lustrous, green, sparsely puberulent to glabrous above and very closely white-canescent with a vestiture of tightly curled hairs (fig. 2b) except along the midribs beneath. Marginal serrations or crenulations are low, variable in development, often quite reduced, and leaf blades are usually slightly revolute between the teeth. Young stems have similar, low, tightly crinkled hairs that do not completely cover stems, but reveal the underlying red-brown coloration.

The taxon is known from the Sierra Jimulco in southwestern Coahuila and the Sierra del Rosario in adjacent northeastern Durango (fig. 9). The two populations are separated by about 75 km and are similar in most characteristics, including vestiture and petiole length. They exhibit some differences in leaf shape, those from the Sierra Jimulco having narrow, more linear-lanceolate leaves with revolute margins and relatively few teeth (fig. 11e) while plants from the Sierra del Rosario tend to have broader, more elliptical leaves with more distinct serrations along their more plain

margins, and the leaf blades tend to be more folded along the midvein (fig. 11f). Leaves of plants from the Sierra Jimulco are somewhat similar to those of subsp. *sonorensis*, but they are smaller, only 2 – 6 cm long, the shortest in the genus, 4 – 8 mm wide, whereas those of subsp. *sonorensis* are 5 – 12 cm long and 6 – 12 mm wide. The patterns of vestiture are also similar in the two taxa, except vestiture of subsp. *retherfordii* is less dense and of lower stature than that of subsp. *sonorensis*. Also, subsp. *sonorensis* occurs at lower elevations, below 1500 m on igneous-derived soils, while subsp. *retherfordii* occurs above 1800 m on limestone soils.

Vauquelinia californica subsp. *retherfordii* occurs in izotal to chaparral scrub in limestone canyons and hillsides from 1800 to 3100 m elevation in association with *Garrya*, *Lindleya*, *Rhus virens*, *Arctostaphylos*, *Quercus*, *Yucca canerosana*, *Agave macroculmis*, *A. parrasana*, and *Fouquieria splendens*.

Representative collections: MÉXICO. **Coahuila**: Sierra de Jimulco, to 3 km N of Mina San José, near 25°06′N, 103°13′W, 27 Sep 1972, *Chiang, Wendt & M.C. Johnston 9548b* (LL); Sierra de Jimulco, N-facing cliffs, near 25°11′N, 103°12′W, 27 Jun 1973, *M.C. Johnston, Wendt & Chiang 11492* (LL); 27 (air) mi SE of Torreon, N side of Sierra Jimulco, S of La Rosita, 25°13′N, 103°13′W, *Henrickson 15874* (TEX). **Durango**: N end of Sierra del Rosario, SW of Mapimí, 25°43′N, 103°57′W, 2 Nov 1972, *Wendt, Chiang & M.C. Johnston 10027* (LL); NW third of Sierra Rosario, near 25°42′N, 103°57′W, 25 Jun 1973, *M. C. Johnston, Chiang & Wendt 11470* (LL).

2d. Vauquelinia californica (Torr.) Sarg. subsp. **pauciflora** (Standl). Hess & Henrickson stat. et comb. non. *Vauquelinia pauciflora* Standl. Proc. Biol. Soc. Wash. 31:132. 1918. Type: MÉXICO. Sonora: Guadalupe Canyon, ne Sonora [probably from southern Cochise Co., Arizona], 3 Oct 1893, *Mearns 2535* (holotype: US!).

Multi- to single-stemmed shrubs, small trees 2 – 4(– 8) m tall; young stems initially closely to loosely tomentulose-villous with tightly crinkled hairs 0.1 – 0.2 mm long, tardily glabrate with persisting short curled puberulence or glabrate. Leaf blades lanceolate, oblong-lanceolate to elliptic, oblong-elliptic, occasionally oblong-ovate, rarely oblanceolate, (2.2 –)3 – 7.5(– 9) cm long, (6 –)8 – 14(– 20) mm wide, [leaf blade length-width ratio (2.8 –)3.5 – 6.5(– 8.6)], coriaceous, 0.2 – 0.3 mm thick, acute, obtuse, rounded or emarginate by dieback, mucronate at tip, abruptly, usually obliquely cuneate to subrounded, occasionally rounded at base, at margins uniformly, closely crenulate, serrulate or doubly crenulate, serrulate with (2 –)4 – 8(– 9) gland-tipped teeth per 1 cm, crenulations low, rounded, (0.1 –)0.2 – 0.4 mm long, sometimes scarcely evident, occasionally more acute, ascending 0.5 – 0.7 mm long, often with dark glands in axils or along margins between teeth; lamina green to yellow-green with yellow mid-secondary veins, glabrate or puberulent

along lower midvein, dull green above, more yellow- to gray-green, with raised yellow, rarely reddish midveins, glabrous or persistently puberulent along midrib beneath; petioles (1.5 −)4 − 16(− 22) mm long, [0.06 −)0.1 − 0.25(− 0.34) times as long as leaf-blades], puberulent throughout or adaxially, occasionally glabrate, 0.85 − 1.2(− 1.4) mm thick, wings thin or broad and tapering with 2 − 7 pair of caducous glands along margins. Compound corymbs 1.5 − 5 cm long, 1.7 − 7 cm wide; lower peduncles 7 − 25 mm long; pedicels-peduncles closely puberulent with coiled hairs to 0.1 mm long to glabrate; bracts-bracteoles lanceolate to subulate, 1.5 − 8 mm long, glandular along margins; hypanthia 1.5 − 2.5 mm long, 2.5 − 3.3 mm wide, to 4.5 mm wide in fruit, puberulent, tardily glabrate outside, glabrous to sericeous inside; sepals 1.1 − 2.2 mm long, 1.4 − 2.0 mm wide, mucronate, margins thin, without sessile glands, puberulent to glabrate outside, villous throughout or only along margins and tip inside; petals oblong-obovate, oblong-ovate to broadly elliptic, 3.4 − 5.4 mm long, 2.4 − 3.4 mm wide, persistent or not; filaments (2.5 −)3 − 6 mm long; anthers 0.8 − 1.1 mm long, to 1.6 mm long wet; styles 1.7 − 2 mm long. Capsules (4.5 −)5 − 6 mm long, 3.5 − 4(− 4.5) mm wide; seeds 3.8 − 5.0 mm long, 1.1 − 1.4 mm wide; embryos 1.8 − 2.4 mm long, 0.9 − 1.2 mm wide. (figs. 9, 12).

Vauquelinia californica subsp. *pauciflora* is characterized by its mostly lanceolate, oblong-lanceolate, crenulate- to serrulate-margined, concolorous leaf blades that tend not to be lustrous above and tend to be glabrate except along the lower midvein on both surfaces and the petioles. The taxon is easily separable from subspecies *sonorensis* and *retherfordii*, as the latter two subspecies at all times have permanently concolorous, more linear, linear-lanceolate leaf blades. Its separation from subsp. *californica* is more difficult, as leaves of individuals of subsp. *californica*, particularly those from populations north and east and in the Superstition Mountains in Pinal and neighboring Maricopa and Gila counties, also tend to become completely glabrate in time, and in this glabrescent characteristic, are identical with subsp. *pauciflora*. Those glabrescent-leaved populations of subsp. *californica*, however, tend to have larger leaves and blend directly into populations of subsp. *californica* with canescent lower leaf surfaces that also tend to have larger leaves than in subsp. *pauciflora*. The factor that prompts us to recognize the taxon *pauciflora* is that the northernmost populations of subsp. *pauciflora* in extreme southeastern Arizona and adjacent New México have relatively small, thickened leaves and small inflorescences (fig. 12a − b), perhaps reflecting the aridity of their habitat, and in this character state are easily distinguished from adjacent populations of subsp. *californica*. Populations of subsp. *pauciflora* from Durango

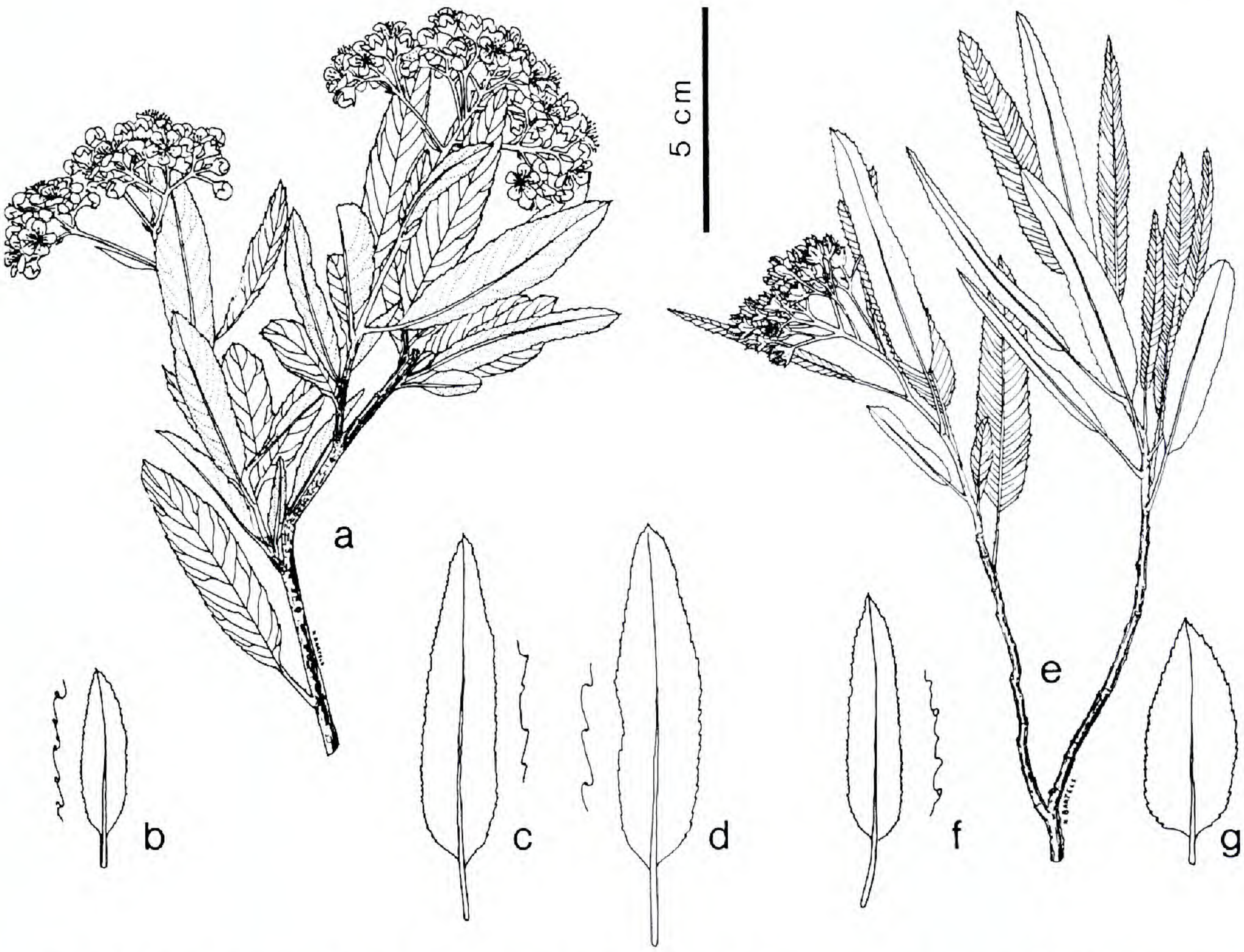


Fig. 12. *Vauquelinia californica* subsp. *pauciflora*. a.—Young stem showing leaves and inflorescences. Collection from extreme southeastern Cochise County, Arizona. *Hess & Wilhelm 4261*. b-d.—Leaf outlines with expanded portions of margins showing leaf variation. b.—Plants from Arizona have very small relatively thickened leaves. *Hess & Wilhelm 4261*. c-d.—Plants from eastern Durango have much larger leaves and are similar to glabrate populations of *V. c.* subsp. *californica*. c.—From near Palmito, *Hess & Wilhelm 4322*. d.—From 42 km S of La Zarca, *M.C. Johnston et al 11436*. e.—Young stem of collection from central Coahuila near Cuatro Ciénegas showing more oblong-lanceolate leaves. *Pinkava et al 6020*. f.—Leaf of same Pinkava collection with expanded margin. g.—Outline of broadly oblong-ovate leaf with short petiole from upper slopes of Sierra San Marcos considered as possible intergrade with *V. corymbosa* subsp. *karwinskyi*. *Engard & Getz 343*. Magnifications as indicated, vertical bar = 1 cm for leaf margin enlargements.

occurring in grassland-scrub habitats, however, have larger, slightly thinner leaves than the Arizona-New México populations (fig. 12c−d), and in this character approach subsp. *californica*. Perhaps the glabrous-leaved populations of subsp. *californica* should also be included in subsp. *pauciflora*, but this, we feel, would put too much weight on the single vestiture character. Whether the glabrescent leaf character state present in the northern populations of subsp. *californica* is derived from the southern populations here placed in subsp. *pauciflora* or is an idependently derived character state is unknown. Our classification represents a workable, perhaps artificial, division between these closely related taxa and implies

that the northern glabrate populations of *V. c.* subsp. *californica* have been independently derived.

Over its range there is an expected amount of variation. As noted above, populations from the arid desertic hillsides in Arizona and New Mexico tend to have shorter, narrower, thicker leaf-blades and shorter petioles than those from grassland habitats in eastern Chihuahua and Durango. The Chihuahua and Durango specimens are also more consistently glabrous. Some collections from Coahuila show intergradation with subspecies of *V. corymbosa*. The collection of *Engard & Getz 342* (fig. 12g) from the Sierra San Marcos southeast of Cuatro Ciénegas has more oblong-ovate leaves to 20 mm wide and very short, thickened, reddish petioles, and in those characters, approaches *V. corymbosa* subsp. *karwinskyi* and subsp. *latifolia* of nearby Tamaulipas. In its fine marginal toothing, however, the Engard & Getz collection is more similar to other collections of subsp. *pauciflora* from the area. There is very strong and evident intergradation of subsp. *pauciflora* with *V. corymbosa* subsp. *heterodon* from the nearby Sierra Paila in south-central Coahuila as is discussed under the latter taxon. These collections tend to have the long leaf-blades and long petioles of subsp. *heterodon*, combined with the tighter marginal toothing of subsp. *pauciflora*.

The type collection of subsp. *pauciflora* was made by Mearns in 1893 during the Mexican-United States Boundary survey. The label states "Guadalupe Canyon, Sonora", but the collection is doubtfully from México, as suitable rocky limestone habitats are lacking south of the border (Wells and Johnson 1964).

As circumscribed subsp. *pauciflora* ranges from Cochise County, Arizona and adjacent Hidalgo County, New Mexico, with isolated populations in northeastern Sonora, southern Chihuahua, and northern Durango, and in central Coahuila in the mountains around Cuatro Ciénegas and southward, where it occurs in mostly semi-arid to arid limestone hillsides from 1400 – 2300 m elevation (fig. 9). Its wide distribution on both sides of the Chihuahuan Desert indicates that it probably occurred throughout the Chihuahuan Desert region during the Holocene. It occurs in arid chaparral-desert scrub in association in limestone substrates with *Mortonia scabrella*, *Parthenium incanum*, *Fouquieria splendens*, *Nolina microcarpa*, *Agave palmeri*, *Trichostema arizonicum*, *Juniperus monosperma*, *Juniperus spp.*, *Prosopis glandulosa*, *Rhus virens*, *Purshia mexicana*, *Mimosa biuncifera*, and species of *Berberis*, *Ephedra*, *Quercus*, *Agave*, and *Yucca*.

Representative collections: U.S.A: Arizona. **Cochise Co.**: Hill, 5 mi NW of Guadalupe Canyon, 27 May 1952, *Blakley & McCleary 1262* (ASU); 24 mi E of Douglas, Guadalupe Canyon, 13 Jun 1970, *Hess 2667* (MOR); same area, 23 Apr 1975, *Hess & Stickney 3440* (MOR); same area, 3 Jun 1978, *Hess & Wilhelm 4261* (MOR). New Mexico: **Hidalgo**

Co.: near New Mexico line, 6 Oct 1944, *Hershey 3377* (GH); 29 mi E of Douglas, Guadalupe Canyon, 25 Apr 1975, *Hess & Stickney 3445* (MOR).

MÉXICO: **Chihuahua**: 9.5 km S of Valle de Zargoza on road to Hidalgo de Parrál, 27°24′N, 105°49′W, 21 Jun 1973, *M.C. Johnston, Wendt & Chiang 11424* (LL). *Coahuila*: 8 km W of Cuatro Ciénegas, slopes of Sierra de la Madera, 26°58′N, 102°08′W, 5 Aug 1973, *M.C. Johnston, Chiang & Morafka 12081a* (LL); Sierra de San Marcos, opposite Los Fresnos, 4 – 5 Apr 1969, *Pinkava et al. 6020* (ASU, NY); Top of Sierra San Marcos, W of Reynolds Mine Headquarters; 12 Jul 1974, *Engard & Getz 342* (ARIZ, LL). **Durango**: Indé, Jun 1927, *Reko 5145* (F, US); W slope of Sierra de Zarca, 15 mi E of Palmito Dam, 19 Sep 1938, *I.M. Johnston 7771* (GH); 12 mi W of La Zarca towards El Palmito, 28 Jul 1959, *Straw & Forman 1723* (MICH, RSA, UC); 13 Mi E of La Zarca, 17 Jun 1955, *M.C. Johnston 2596a* (MICH, TEX-2 sheets); 42 km S of La Zarca, 10.5 km N of Alamilla de Galeana, 25°27′N, 104°36′W, 22 Jun 1973, *M.C. Johnston, Wendt & Chiang 11436* (LL); 14.9 rd mi NW Los Herreras in Cañon de Potrero, 25°15′N, 105°39′W, 10 Jul 1983, *Corral D. & Worthington 11024* (MO). **Sonora**: Cañon de la Bota, N end of Sierra el Tigre, ca 34 air km ESE of Esqueda, 30°36′N, 109°13′W; 31 Jan 1982, *VanDevender, Yatskievych 82-60* (ARIZ).

3. Vauquelinia corymbosa Humboldt & Bonpland

Multi-stemmed shrubs to single-trunked trees 1.5 – 7(– 10) m tall; young stems initially tomentulose with tightly crinkled hairs, soon to tardily glabrate, sometimes with persistent, close puberulence of coiled hairs that fall with epidermis; bark gray, dark gray, smooth, often plaited in vertical strips on larger trunks. Leaves erect-ascending or drooping on short to elongate petioles; leaf-blades linear to broadly ovate, (2.4 –)3 – 12(– 17) cm long, (3 –)10 – 40(– 65) mm wide, subcoriaceous to rigidly coriaceous, acute to rounded, mucronate at tip, obliquely cuneate to truncate-subcordate with margins decurrent along adaxial petiole at base, at margins plain to variously crisped, variably serrate, doubly serrate to serrulate with 3 – 21, mostly acute-acuminate, ascending to divergent serrations per 5 cm, their number depending on the extent of development of secondary serrations, serrations often variable among leaves of a shoot, upper serration margins variably concave, straight or convex, lower margins concave, straight or sigmoid, corneous, usually terminating with a distinct, sessile, terminal, caducous gland, similar glands sometimes present in axils of teeth and along margins between teeth, gland bases often dark, persisting; lamina densely villous-tomentose when young, glabrate, green, yellow-green, lustrous, with slightly impressed, yellowish midvein above, glabrate, subglabrate, sometimes developing local accumulations of wax, more yellow- to gray-green, with yellowish midvein raised, secondary and smaller veins at least visible beneath; petioles (4 –)10 – 40(– 65) mm long, thick or slender, yellow-green or tinged with red, canaliculate, adaxially winged by decurrent leaf margins

in distal one-half or two-thirds, wing margins with scattered sessile, caducous glands; stipules narrowly deltate, 0.5 – 1 mm long, glabrous to tardily glabrate, obscurely gland-margined. Compound corymbs 2 – 7(– 10) cm long, 2.5 – 9(– 10.5) cm wide, often aggregated at stem tips, each terminating a lateral branch; pedicels-peduncles yellow-green to reddish-brown below, puberulent, floccose to glabrate; hypanthia obconic to hemispheric, densely villous with crinkled hairs in bud, variously glabrescent, often lustrous outside, usually glabrous, nectariferous below filaments, sericeous around ovary inside; sepals broadly ovate, deltate, 1.2 – 2.5(– 3.5) mm long, 1.5 – 2(– 2.5) mm wide at base, strongly mucronate, margins thin, often with sessile glands, variously villous inside with hairs usually showing along margins; petals oblong-ovate, oblong-obovate, (2.4 –)4 – 5.6 mm long, 1.8 – 4 mm wide, rounded to occasionally retuse at tip, broadly cuneate to rounded, often above a broad claw 0.2 – 0.5 mm long at base, initially villous-tomentulose where exposed in bud but usually glabrate, sometimes loosely floccose at tip at anthesis; stamens 18 – 20; filaments 2.7 – 6.5 mm long; anthers 0.6 – 1.1 mm long, to 1.5 mm long wet; styles 1.3 – 2.4 mm long. Capsules 4.5 – 7.5 mm long, 3 – 6.5 mm wide; seeds (3.5 –)4 – 6 mm long, 1 – 1.6 mm wide (including wing); embryos 1.6 – 3 mm long, (0.7 –)1 – 1.3 mm wide (figs. 14 – 19).

With six subspecies occurring from Texas, Coahuila and south along the Sierra Madre Oriental to Hidalgo (fig. 13).

KEY TO SUBSPECIES OF *VAUQUELINIA CORYMBOSA*

A. Petioles mostly 25 – 55(– 65) mm long.
  B. Leaf-blades oblong-lanceolate, oblong-elliptical, oblong-ovate, to broadly ovate, (4 –)6 – 10(– 11.5) cm long, serrate to partially doubly serrate with 6 – 10(– 14) teeth per 5 cm; Hidalgo to Querétaro . . . . . 3a. *V. corymbosa* subsp. *corymbosa*
  BB. Leaf-blades lanceolate to oblong-lanceolate, mostly 7 – 14(– 17) cm long, coarsely, doubly serrulate with (6 –)8 – 19(– 21) teeth per 5 cm; eastern Coahuila and adjacent Nuevo León . . . . . 3b. *V. corymbosa* subsp. *heterodon*

AA. Petioles mostly 5 – 28 mm long, rarely longer.
  B. Leaves narrowly linear, oblong-linear, 7 – 13(– 17) cm long, (3 –)5 – 9(– 12) mm wide, strongly serrate to partially doubly serrate; Texas, eastern Chihuahua to central Coahuila. . . . . 3c. *V. corymbosa* subsp. *angustifolia*
  BB. Leaves oblong-lanceolate to ovate, broader in the lower half, (1.2 –)3 – 9(– 13) cm long, 10 – 45(– 65) mm wide; San Luis Potosí, Nuevo León to Tamaulipas.
    C. Leaves oblong-lanceolate, oblong-elliptical, oblong-ovate or ovate, 3 – 9(– 13) cm long, 10 – 25(– 36) mm wide, not

glaucous, moderately coriaceous; petioles 5 – 24(– 34) mm long, moderately thin, 0.7 – 1.5(– 2) mm wide, winged distally or nearly to base by decurrent leaf margins; San Luis Potosí, western Tamaulipas to Nuevo León.

D. Inflorescence, young stems, and petioles usually glabrate; petioles (8 –)12 – 18(– 34) mm long, winged in distal half; leaf-blades (4 –)5 – 19(– 13) cm long; San Luis Potosí to western Tamaulipas. . . 3d. *V. corymbosa* subsp. *karwinskyi*

DD. Inflorescence, young stems, petioles persistently puberulent; petioles 4 – 9(– 13) mm long, winged to near the base; leaf-blades 3 – 5 (rarely to 7) cm long; eastern Coahuila to Nuevo León. 3e. *V. corymbosa* subsp. *saltilloensis*

CC. Leaves broadly oblong-ovate to broadly ovate, (3 –) 5 – 8(– 12.5) cm long, (15 –)22 – 40(– 65) mm wide, glaucous, strongly coriaceous; petioles stout, (7 –)10 – 15(– 18) mm long, 1.2 – 2.5 mm thick, usually tinged with red, not winged by decurrent leaf markings; western Tamaulipas. . . . . 3f. *V. corymbosa* subsp. *latifolia*

3a. VAUQUELINIA CORYMBOSA Humb. & Bonpl. subsp. CORYMBOSA, Pl. Aequin. 1(6):140, pl. 40. 1807. TYPE: MÉXICO. HIDALGO: juxta Actopan, Aug 1803, *Humboldt & Bonpland s.n.* (HOLOTYPE: P – microfiche!; ISOTYPE: F! – fragment from P).

Small rounded trees to multi-stemmed shrubs 2 – 6(– 8) m tall; young stems initially tomentulose, soon or rarely tardily glabrate. Leaves ascending or drooping; leaf-blades oblong-lanceolate to narrowly lanceolate to narrowly elliptical, oblong, narrowly oblong, oblong-ovate, broadly ovate, (4.2 –)6 – 10(– 11.5)[– 12.7] cm long, (8 –)11 – 28(– 43) mm wide, [length-width ratio (1.7 –)2.5 – 7(– 10.5)], thinly coriaceous, 0.18 – 0.24 mm thick, attenuate to obtuse (rarely retuse), acuminately mucronate at tip, narrowly to abruptly, often obliquely cuneate at base, at margins moderately to strongly crisped, irregularly, sharply serrate to partially doubly serrate with (6 –)7 – 10(– 14) teeth per 5 cm, [(1 –)2 – 3(– 4) per 1 cm], larger serrations (1 –)1.5 – 4(– 5) mm long, acute-acuminate, divergent or often inwardly hooked or curved at tips, often with sessile glands in axils of serrations and/or between serrations occasionally manifested as reduced secondary serrations 0.5 – 1.0 mm long; lamina glabrous, dark green with yellow mid and secondary veins, lustrous above, more yellow green with raised yellow midvein, glabrous, sometimes accumulating waxy deposits beneath; petioles (14 –)25 – 55 mm long, [(0.23 –)0.3 – 0.6(– 0.75) times as long as leaf blade], slender, 0.7 – 1.0(– 1.2) thick, very narrowly winged in distal 3 – 15 mm, wings with obscure glands on margins, tomentulose, glabrate, rarely puberulent on adaxial surface. Compound corymbs 2.5 – 7 cm long,

3.5 – 9.5 cm wide; lower peduncles 10 – 42 mm long; pedicels-peduncles glabrous or puberulent-floccose, glabrate, upper bracts-bracteoles 1 – 4 mm long; hypanthia 1.5 – 2.5 mm long, 2.5 – 3.5 mm wide, to 4.5 mm wide in fruit, floccose, sparsely villous to glabrate outside; sepals 1.2 – 2(– 2.5) mm long, to 1.6 – 2 mm wide, bluntly mucronate, rarely glandular along thin margins, puberulent-floccose to glabrate outside, densely villous at tip and along margins inside; petals oblong-ovate, oblong-obovate, (3.5 –)4 – 5 mm long, 2.5 – 3.4 mm wide, broadly clawed at base; filaments 2.7 – 5 mm long; anthers 0.9 – 1.0 mm long, to 1.5 mm long wet; styles 1.3 – 2 mm long. Capsules 5 – 6.2 mm long, 3.5 – 4.5(– 5) mm wide; seeds 4.4 – 4.8 mm long, 1 – 1.3 mm wide; embryos 2 – 2.5 mm long, 0.7 – 1.1 mm wide. (figs. 13, 14).

Vauquelinia corymbosa subsp. *corymbosa* is a highly variable taxon, characterized by moderately slender young stems, erect to spreading or drooping leaf blades borne on relatively long, slender petioles mostly 25 – 55 mm long (0.3 – 0.75 times as long as the leaf blades). Leaf blades are highly variable in outline, ranging from narrowly lanceolate to broadly oblong-ovate and are usually moderately to strongly crisped, coarsely serrate, occasionally partially doubly serrate, and marginal serrations may be divergent or ascending, frequently upcurved at the tip (fig. 14).

Some specimens with long, narrow leaf blades and sharp, divergent serrations [*L. Gonzalez Q. 2393* (fig. 14c), *Hess & Wilhelm 4371* (fig. 14g), *F. Brizuela 1103*, and *C.T. Mason Jr. 2621*] approach *V. corymbosa* subsp. *heterodon* except for the tendency to lack secondary serrations and their relatively short petioles (fig. 14 c,g). In leaf-blade shape, subsp. *corymbosa* approaches subsp. *karwinskyi*, but the latter taxon has distinctly shorter petioles (fig. 17). In some plants from the Cerro de Santa María near Atotonilco el Grande, northeast of Pachuca, Hidalgo, largest leaf blades are more broadly oblong-ovate to broadly ovate, (42 –)52 – 85 mm long, (14 –)20 – 43 mm wide, mostly 1.7 – 3.3(– 4.7) times longer than wide (fig. 14b) and in this broad leaf-blade characteristic differ from other populations of subsp. *corymbosa*. However, a population collection by Hess from the site (*Hess 4376*) reveals that the broad leaf-blade characteristic is not consistent throughout the population, and the population is thus not distinguished nomenclaturally.

The common name of "Palo Alto" is recorded on a specimen from Querétaro by McVaugh (*10355*). The names "Arbol prieto, Guayúl, Guayule, Palo prieto, Palo verde, Ucas" are listed for this taxon in Martinez (1979). Hess (*4376*) recorded the name "Palo Real" on a specimen from Atotonilco, Hidalgo.

Vauquelinia corymbosa subsp. *corymbosa* is restricted to limestone, xeric to

Fig. 13. Distribution of subspecies of *Vauquelinia corymbosa* and of *V. australis* in México and southwestern United States.

mesic hillsides in Matorral Xerofilo to just below the pine belt in valleys and mountains of northern Hidalgo and Querétaro (fig. 13) from 2000 to 2700 m elevation, where it occurs in association with species of *Acacia*, *Brahea*, *Helietta*, *Juniperus*, *Karwinskia*, *Leucophyllum*, *Opuntia*, *Satureja*, *Rhus*, *and Robinia*.

Representative collections: MÉXICO. **Hidalgo**: Ixmiquilpan, Aug 1905, *Rose, Painter & Rose 9159* (GH, NY, US); 12 mi S of Ixmiquilpan, 29 Oct 1966, *C.T. Mason Jr., 2621* (ARIZ); 2.5 km al ENE de Don Guiñó, Mcpio. de Alfayayucan, 4 May 1974, *F. Brizuela*

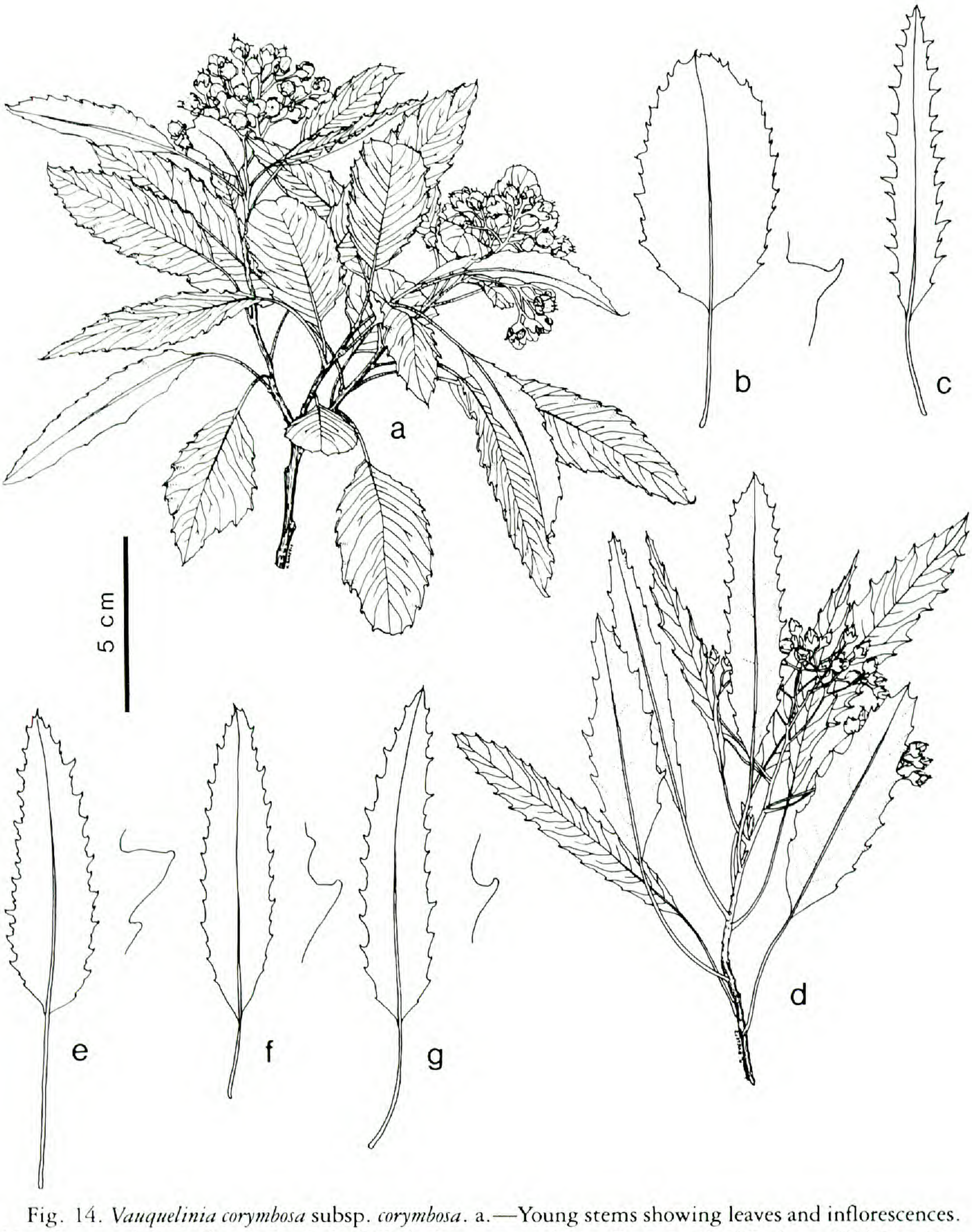


Fig. 14. *Vauquelinia corymbosa* subsp. *corymbosa*. a.—Young stems showing leaves and inflorescences. Note long petioles and variation in leaf-blade shape on specimen. From north of Pachuca, Hidalgo. *Hess & Byrne 4655*. b.—Broadly elliptical leaf from same specimen as in a. c.—Narrow leaf with some double serrations as in subsp. *heterodon*. From NNE of Actopan, Hidalgo. *L. Gonzalez Q. 2393*. d.—Young stem of plant from N of Bernal, Querétaro showing similar long petioles but narrower leaves. *Hess & Wilhelm 4371*. e-g.—Leaf outline and expanded margins from specimens from Querétaro showing variation in marginal serrations. e.—With well developed double serrations from between Pilon and Pinol de Amoles. *McVaugh 10355*. f.—With partial development of double serrations from near Bernal. *Rzedowski 25567*. g.—With single serrations from near Bernal. *Hess & Wilhelm 4371*. Magnifications as indicated, vertical bar = 1 cm for leaf margin enlargements.

1103 (CAS, MEXU); Cerro San Miguel, 14 km al NNE de Actopan, 6 May 1965, *L. González-Q. 2393* (SD 2 sheets, F, LL, MICH); NW crest of Cerro Soyutla, 6 km S of Atotonilco, 25 Sep 1976, *Clausen 76-48* (MICH, MEXU, US); Cerca de San Cristobal, Mcpio. de Cardonál, 21 Mar 1977, *Rzedowski 346734* (ARIZ, CAS, MICH); Cerro de Santa Maria, cerca de Laguna, Mcpio. de Atotonilco el Grande, 25 Nov 1973, *Rzedowski 31515* (ENCB, MEXU, MO, MICH); 5 mi N of Atotonilco, 16 Jun 1978, *Hess & Wilhelm 4376* (MOR). **Querétaro**: above Pilon on road to Pinal de Amoles, 24 Apr 1949, *McVaugh 10355* (DS, GH, LL, MEXU, MICH, MO − 2 sheets, TEX, UC); 13 mi NE of Peña Blanca, 20°40′W, 99°40′W, 5 Jun 1919, *Hess & Byrne 4644* (MOR); 3 km al NE de Bernal, sobre el camino a Toliman, 23 Mar 1968, *Rzedowski 25567* (ARIZ, DS, LL, MICH − 2 sheets), US).

3b. VAUQUELINIA CORYMBOSA subsp. **heterodon** (I.M. Johnston) Hess & Henrickson comb. et stat. nov. *Vauquelinia heterodon* I.M. Johnston. J. Arnold Arbor. 21:258. 1940. TYPE: MÉXICO. COAHUILA: road from Monclova south to Saltillo, 40 km s of Monclova, Sierra Gavia, 5 mi n of Saucillo, frequent in canyon slopes and along canyon bottom, 10 − 20 ft high, 27 − 30 Aug 1938, *I.M. Johnston 7217* (HOLOTYPE: GH!; ISOTYPE: US!).

Small trees to multi-stemmed shrubs 2 − 6(− 10) m tall; young stems initially tomentulose, soon or rarely tardily glabrate. Leaves ascending; leaf blades lanceolate, oblong-lanceolate, (5 −)7 − 14(− 17) cm long, (7 −)10 − 23(− 25)[− 30] mm wide, [leaf length-width ratio 4.3 − 7.5(− 9)], coriaceous, 0.18 − 0.3 mm thick, gradually tapering to an attenuate tip, abruptly to gradually, often obliquely cuneate at base, at margins plain or strongly crisped, coarsely, sharply doubly serrate with (6 −)8 − 19(− 21) serrations per 5 cm, [2 − 3(− 4) per 1 cm]; larger serrations divergent or ascending, acute or acuminate below a rather blunt tip, tipped with a minute, caducous gland; larger serrations 1 − 3(− 5)[− 7] mm long, secondary serrations 0.4 − 1 mm long, mostly ascending, commonly with small glands in axils of both large and small serrations; lamina glabrate, dark green with yellow mid and secondary veins, lustrous above, more yellow- or gray-green with raised yellowish midvein, usually glabrous, rarely with accumulations of wax beneath; petioles (15 −)22 − 45(− 65) mm long, [(0.17 −)0.2 − 0.35(− 0.4) times as long as leaf blade], moderately slender, 0.8 − 1.2(− 1.5) mm wide distally, yellow to yellow-maroon, glabrous to sparsely puberulent, narrowly winged in distal 1 − 3(− 4) cm, wings with small caducous glands. Compound corymbs 3 − 7(− 10) cm long, 3 − 8(− 12) cm wide; lower peduncles 12 − 35 mm long, pedicels-peduncles glabrous or puberulent-floccose, glabrate; upper bracts-bracteoles subulate, (1 −)2 − 4.5 mm long with glands along margins; hypanthia (1.5 −)2 − 2.5 mm long, to 2.5 − 3.5 mm wide, to 5.5 mm wide in fruit, glabrate outside; sepals 1.3 − 2.2(− 3.5) mm long, to 1.5 − 2.2(− 2.5) mm wide, strongly

mucronate, glandular along thin margins, floccose, glabrate outside, usually densely villous at tip and along margins inside; petals broadly oblong-ovate, (3.5 –)4 – 5.3 mm long, (2.5 –)3.2 – 4 mm wide; filaments 2.7 – 5.7 mm long; anthers 0.9 – 1.1 mm long, to 1.5 mm long wet; styles 2 – 2.4 mm long. Capsules (4.5 –)5 – 7 mm long, 4 – 6.5 mm wide; seeds 4.5 – 5.5 mm long, 1.2 – 1.6 mm wide; embryos 2.3 – 3 mm long, 0.9 – 1.3 mm wide (figs. 13, 15).

Vauquelinia corymbosa subsp. *heterodon* is characterized by its relatively long, narrowly lanceolate to oblong, sharply doubly serrate leaf blades mostly 8 – 15 cm long, 10 – 23 mm wide borne on long petioles 22 – 45(– 65) mm in length (fig. 15). Most collections from throughout its range fall readily into this pattern, with variation expressed in development and orientation of leaf serrations, the degree of crisping noted in the margins (the holotype specimen has strongly crisped leaf-blade margins), the presence or absence of sessile caducous glands on sepal margins and leaf serration axils, in mature capsule and inflorescence size and development, and persistence of vestiture. Mature stems, leaves, inflorescences, and hypanthia of most collections appear glabrate; occasional plants (*Hinton 16521*) retain some tightly coiled hairs on inflorescences, stems, and petioles.

Several specimens bordering the southeastern edge of the Bolsón de Mapimí approach *V. californica* subsp. *pauciflora* in their reduced toothing and shorter petioles. A collection by *M.C. Johnston et al. (11684*, fig. 15e) from the north side of the Sierra Paila that lies some 70 km south of recent collections of *V. californica* subsp. *pauciflora*, has moderately small leaves, 4.5 – 8.5 cm long, 10 – 17 mm wide with reduced, poorly developed marginal serrations 0.5 – 1.5 mm long and petioles only 17 – 39 mm long. Although this collection has reduced leaf serrations, it can be assigned to subsp. *heterodon*, as it has moderately long petioles and a moderate development of double serrations on some leaves. Another intermediate specimen by *Wendt et al. (10110B*, fig. 15f), 20 km to the south in the same range, has even narrower leaves, 4.5 – 8.2 cm long, 5 – 11 mm wide with reduced marginal serrations seldom over 0.5 mm long that scarcely show the characteristic double serrations of subsp. *heterodon*. The collection, however, has petioles 16 – 32 mm long and in that character again approaches subsp. *heterodon* most strongly, but shows strong intergradation towards *V. californica* subsp. *pauciflora* and is considered an intermediate between the taxa. Specimens of Purpus (*4945*, fig. 15g – h) from the Sierra Parras also exhibit some intermediacy towards *V. c.* subsp. *pauciflora*, having shorter leaf blades, less well developed double serrations, and reduced petiole lengths in some leaves. But these collections show only

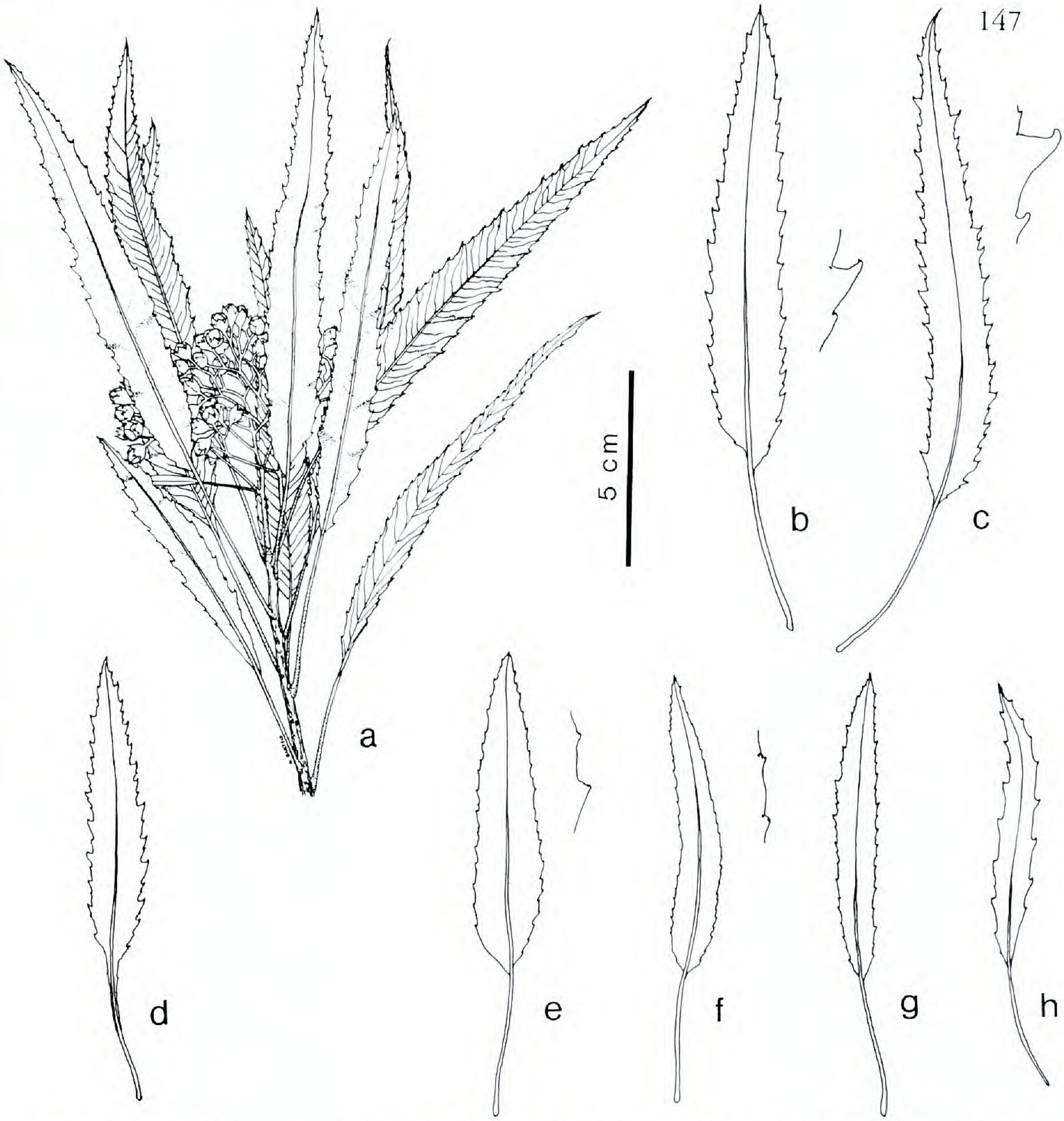


Fig. 15. *Vauquelinia corymbosa* subsp. *heterodon*. a.—Young stem with leaves and inflorescence. Near type locality in San Lazaro Pass in Sierra Gavia, Coahuila. *Hess & Wilhelm 4354*. b-h.—Leaf outlines with expanded section of margins showing variation in leaf size and marginal serrations. b.—With reduced secondary serrations from type locality. *Spetzman & Zapien 1353*. c.—With well developed double serrations from Villa de Garcia near Monterrey, Nuevo Leon. *Hernandez et al A-88*. d.—Reduced leaf from isolated population near San Carlos, Tamaulipas. *Bartlett 10207*. e-f.—Collections from Sierra Paila, NW of Saltillo, Coahuila have long petiole but fine toothing and are considered as intergrades with *V. californica* subsp. *parviflora*. e.—*Johnston, Wendt & Chiang 11684*. f.—*Wendt, Chiang & Johnston 10110B*. g-h.—Leaves from collection near Parras de la Fuente, Coahuila, showing small size, uncharacteristic single serrations. Both *Purpus 4945*. Magnifications as indicated, vertical bar = 1 cm for leaf margin enlargements.

slight convergence towards *V. c.* subsp. *pauciflora* in comparison with some collections from the northern Sierra de Paila.

Vauquelinia corymbosa subsp. *heterodon* occurs on limestone hillsides and canyons of central Coahuila from the mountains near Monclova south to the

Sierra de Paila northeast of Saltillo and in the Sierra de Parras south of Parras de la Fuente and in adjacent Nuevo León near Lampazos and the mountains northeast of Monterrey and in an isolation locality in the Sierra de San Carlos in west central Tamaulipas (fig. 13). It occurs in arid canyon scrub, oak woodland and chaparral from 650 to 2100 m elevation with a wide diversity of genera including *Acacia, Anisacanthus, Agave, Brahea, Brickellia, Bumelia, Condalia, Cordia, Dasylirion, Forestiera, Fraxinus, Gochnatia, Helietta, Jatropha, Karwinskia, Leucophyllum, Opuntia, Pistacia, Prosopis, Ptelea, Rhus, Randia, Tecoma, and Viguiera.*

The common names "Serucha" (*fide M.T. Edwards 330*, Lampazos, N.L.), "Lantrisco" (*fide Hinton 16521*, Sierra Paila), "Cercacilla" (*fide Wendt 2000*, NE Tamaulipas) have been noted for the taxon.

Representative collections: MÉXICO. **Coahuila**: Sierra de la Gloria, SE of Monclova, 3 Jul 1939, *Marsh 1923* (F, GH, TEX); Caracól Mts., 21 mi S of Monclova, Aug 1880, *Palmer 329* (AA, GH, MICH, NY, US); San Lazaro, near N entrance of El Puerto de San Lazaro, 16 Jun 1936, *Wynd & Muller 104* (ARIZ, GH, MICH, MO, NY, US); lower end of Canyon of San Lazaro, 31 mi S of Castaños, 14 Oct 1959, *M.C. Johnston 4432* (MEXU, MICH, TEX); 35 (air) mi S of Monclova, Cañón la Gavia on N side of Sierra de la Gavia, 26°21′N, 101°17′W, 2 Aug 1973, *Henrickson 11712* (TEX); Sierra Paila, Valle Seco, 1 Aug 1944, *Hinton 16521* (NY, US); Sierra de Paila, 5 mi W of Rancho La Luz, 14 Jun 1963, *Gentry, Barclay & Arguelles 20058* (US); Sierra de Paila, La Sauceda, 5 May 1967, *Marroquin 1518* (F, MEXU − 2 sheets, TEX); Sierra de la Paila, upper reaches of Cañón Corazón del Toro at Mina la Abundancia, near 25°54′N, 101°38′W, 5 Nov 1972, *Wendt, Chiang & Johnston 10110b* (LL); Mina El Aguirreno, N side of Sierra de la Paila, near 26°05′N, 101°36′W, 5 Jul 1973, *M.C. Johnston, Wendt & Chiang 11684* (LL); Parrás, Oct 1910, *Purpus 4945* (F, GH, MO, US). **Nuevo León**: Rancho Rezendez, Lampazos, 24 Jun 1937, *Edwards 330* (ARIZ, DS, F, MEXU, MO, RSA, TEX); Just E of Cerro Providencia (just SE of Candela) 26°48′N, 100°37′W, 22 Jul 1977, *Wendt 2000* (TEX); N side Sierra del Muerto, Cañón de Potrerillos, 26°01′N, 100°12′W, 16 Mar 1973, *M.C. Johnston, Wendt & Chiang 10241* (LL); 1 km adelante de Villa García, 23 Nov 1955, *Hernandez, Valdez & Miranda A-88* (MEXU); Sierra del Fraile, near Garcia Caves, 5 mi NE of Villa de Garcia, 25°53′N, 100°30′W, 17 Jun 1979, *Hess 4735* (MOR). **Tamaulipas**: Sierra de San Carlos, Cerro de los Armadillos, vicinity of San Jose, 10 Jul 1930, *Bartlett 10207* (F, GH, LL, MICH, US).

3c. Vauquelinia corymbosa subsp. **angustifolia** (Rydb.) Hess & Henrickson comb. et stat. nov. *Vauquelinia angustifolia* Rydb. N. Amer. Fl. 22:260. 1908. Type: MEXICO. Chihuahua: Santa Eulalia Mountains, 27 May 1885, *C.G. Pringle 5* (holotype: US!; isotypes: AA!, F − 2 sheets!, GH!, LL!, NY!, RSA − 2 sheets!, UC − 2 sheets).

Multi-stemmed, erect, ovoid shrubs 1.5 − 3(− 5) m tall; young stems initially tomentulose, soon or tardily glabrate with a close vestiture of crinkled hairs. Leaves ascending, erect to spreading; leaf blades linear to linear-oblong, (3.5 −)6 − 13(− 18.5) cm long, (3 −)5 − 9(− 12)[− 15] mm wide, [length-width ratio (6.5 −)16 − 24(− 37)], coriaceous,

0.2 − 0.32 mm thick, acute, obtuse, often mucronate at tip, gradually, often obliquely cuneate at base, at margins coarsely to obscurely serrate, serrulate, occasionally partially doubly serrate with (3 −)5 − 10 (− 14)[− 20] teeth per 5 cm (0 − 4 per 1 cm), serrations ascending to divergent, 0.2 − 1.5(− 2)[− 3] mm long, acute-acuminate or reduced to rounded crenulations, usually terminating with a sessile, caducous gland with persisting dark base at inside tip, often with a sessile gland in axil of serration and occasionally along margin between major serrations, these sometimes manifested as secondary serrations to 0.5 mm long, rarely entire or serrations unevenly or poorly developed; lamina initially tomentulose with hairs 0.3 − 0.5 mm long, soon or somewhat tardily glabrate, the remaining hairs to 0.1 mm long, green, yellow-green, with yellow mid and secondary veins, glabrate, lustrous above, more yellow-green with yellow, raised midvein beneath; petioles (6 −)9 − 28(− 40) mm long, [(0.07 −)0.1 − 0.2(− 0.33) times as long as leaf blade], glabrous or puberulent adaxially, wings narrow, tapering nearly to base. Compound corymbs 2.5 − 5.5 cm long, (3 −)3.5 − 6(− 7) cm wide; lower peduncles 8 − 27 mm long; pedicels-peduncles glabrate or minutely puberulent with coiled hairs; upper bracts-bracteoles subulate, 0.7 − 3 mm long; hypanthia 1.7 − 2.5 mm high, 2.5 − 3.8 mm wide, to 4.7 mm wide in fruit, initially tomentulose, glabrate or puberulent, floccose outside, glabrous above a sericeous base inside; sepals (1.3 −)1.5 − 2.4 mm long, 1.5 − 2.3 mm wide, acute, bluntly mucronate, glandular along thin margins, glabrate to floccose-villous outside, strongly tomentulose-villous inside and along margins; petals broadly oblong-ovate, ovate, 2.4 − 4.5(− 5.6) mm long, 2 − 3.5 mm wide, broadly clawed at base; filaments 2.6 − 5 mm long; anthers 0.6 − 1.1 mm long, to 1.4 mm long wet; styles 2 − 2.2 mm long. Capsules 5 − 7.5 mm long, 3.7 − 5.4 mm wide; seeds 4.3 − 6 mm long, 1.2 − 1.6 mm wide; embryos 1.6 − 2.4 mm long, 1.0 − 1.2 mm wide. Chromosome number $n = 15$ (Goldblatt 1976). (figs. 13, 16).

Vauquelinia corymbosa subsp. *angustifolia* is characterized by its uniformly narrow linear to oblong-linear leaf blades with coarse marginal serrations (fig. 16). In these features, subsp. *angustifolia* appears most similar to subsp. *heterodon* (fig. 15), but subsp. *angustifolia* has more uniformly narrow leaf blades (3 −)5 − 9(− 12) mm wide, while those of subsp. *heterodon* are more lanceolate to oblong-lanceolate, broader in the lower half, (7 −)10 − 23(− 25) mm wide, and are usually doubly, not once, serrate. The petioles of subsp. *heterodon* also tend to be much longer, (15 −)22 − 45(− 65) mm long versus (6 −)9 − 28(− 40) for subsp. *angustifolia*. *Vauquelinia corymbosa* subsp. *heterodon* also tends to form distinct trees while subsp. *angustifolia* is usually a multi-stemmed shrub.

Throughout its range, subsp. *angustifolia* exhibits considerable diversity in leaf blade size and shape. Plants from the western portions of its range, including those from the type locality, tend to have much broader leaf blades, 8.5 – 12 mm wide (including serrations), with leaf-blade length-width ratios ranging from 6.5 to 12 (fig. 16f – g). In contrast, plants from Texas and southward tend to have narrower leaf blades (3 –)5 – 9, only rarely to 12 mm wide, with leaf blade length-width ratios of (7 –)16 – 24(– 37), with the smallest ratios originating from very narrow, short leaves (fig. 16 b – d). Some of these plants also tend to have more distinctly glabrate inflorescences. Analyses by Hess, however, show no statistically significant differences between these populations.

Occasional plants of very arid exposed habitats have shorter, narrower leaf blades measuring 5 – 9 cm long, 3.5 – 6.5 mm wide, with marginal serrations only 3 – 5 mm apart [*I.M. Johnston & Muller 549*, (fig. 16j)]; others have much longer leaves to 21 cm in total length (including a petiole 2.5 cm long) with serrations up to 17 – 20 mm apart [*I.M. Johnston 9313*, (fig. 16b)]. Generally the number of serrations, measured as the number per 5 cm of margin, is greatest in small leaves with some doubled serrations.

One specimen from the Sierra de los Pinos of northern Chihuahua [*LeSueur 1531*, (fig. 16e)] has very narrow leaf blades, with some leaf blades weakly serrulate and others entire. The entire leaf blades range from 5 to 13 cm in length, 3 – 5 mm in width, with the longest leaves lacking serrations altogether. As in other taxa of the genus, leaf-blade toothing varies considerably. Most specimens have one series of divergent or ascending, acute-acuminate serrations that measure from 0.5 – 1.5 mm long. In some plants, serrations are more pronounced, measuring to 3 mm in length as in *Chiang et al. 8387* (LL), but this is rare. In others, they are reduced to small, rounded, gland-tipped knobs under 0.5 mm long, as in *M.C. Johnston et al. 11310* (fig. 16i). Occasional plants show partial development of secondary serrations, making some leaf blades partially doubly serrate.

Minor variation is also known in flower characteristics, particularly in petal size and shape, with some plants tending to have narrow, more oblong-ovate petals.

Vauquelinia corymbosa subsp. *angustifolia* occurs mostly on limestone, rarely igneous-rock slopes and canyons, and also on gypsum flats from eastern Chihuahua, southern trans-Pecos Texas south to central Coahuila

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Fig. 16. *Vauquelinia corymbosa* subsp. *angustifolia*. a.—Young stem showing narrow leaves and inflorescences. Inserts show flowers. b-j.—Outline drawings of leaves, some with marginal toothing shown expanded, showing variation in shape, size, and petiole length. b.—Typical but very long leaf from Sierra de la Madera, Coahuila. *I.M. Johnston 9313*. c.—Typical narrow leaf from Chisos

Mountains, Texas. *Lundell & Lundell 14606*. d.—Typical leaf from Sierra de Zacatosa, W of Cuatro Ciénegas, Coahuila. *Chiang et al 12100A*. e—Aberrant, entire, very narrow leaf from collection of Sierra de los Pinos in NE Chihuahua. *LeSueur 1531*. f-g.—Collections from western portion of range often have broader laminas. f.—From Santa Eulalia Mountains near Cd. Chihuahua, Chihuahua (type locality). *Pringle 369*. g.—Similar broad leaf from Sierra Morrión in NE Chihuahua. *Chiang, Wendt & Johnston 8387*. h.—Atypical short, broad leaf from collection from SW flank of Sierra del Carmen in N Coahuila. *Chiang, Wendt and Johnston 9271*. i.—Abnormal very short leaf from Sierra de Parra in NE Chihuahua. *Johnston, Wendt & Chiang 11310*. j.—Very reduced, narrow leaf from Sierra Santa Fe del Pino in N Coahuila. *I.M. Johnston & C.H. Muller 549*. Magnifications as indicated, vertical bar = 1 cm for leaf margin enlargements.

(fig. 13), from 1050 to 1500 m elevation, where it occurs in the Chihuahuan Desert canyon scrub and chaparral with genera and species such as *Acacia berlandieri, A. rigidula, Bouvardia, Buddleja, Cercocarpus montanus, Chilopsis linearis, Diospyros texana, Eysenhardtia, Fallugia paradoxa, Fraxinus greggii, Gutierrezia, Juglans, Juniperus, Mimosa, Pinus cembroides, Quercus, Rhus virens, Ungnadia, Viguiera* and *Yucca*.

R.M. Stewart (962, GH) reports the common name of "Barreta" on a collection from northern Coahuila.

Representative collections: U.S.A.: Texas. **Brewster Co.**: Chisos Mts., ridge on E side of Juniper Cañón, 15 – 18 Jul 1921, *Ferris & Duncan 2927* (CAS, DS, NY); Chisos Mts., Blue Creek Canyon, 23 Jun 1931, *Moore & Steyermark 3203* (AA, CAS, DS, MICH, NY, UC); Chisos Mts., Oak Creek Canyon near Camp and the Window, 5 Jul 1937, *Sperry 168* (US); Mid-slopes of Dead Horse Mountains, near Sue Peak, Big Bend Nat. Park, 19 Jul 1952, *Warnock 10778* (LL). **Presidio Co.**: Chinate Mts., 11 Sep 1914, *Young s.n.* (TEX).

MÉXICO: **Chihuahua**. Sierra de Pinos, Dec 1937, *LeSueur 1531* (ARIZ, F, GH, TEX); Sierra de la Parra, across river from Sierra Vieja, 30°00′N, 104°52′W, 13 Jun 1973, *M.C. Johnston, Wendt & Chiang 11310* (LL); Ca 27 mi NE of El Morrión, ca 9 mi NE of RR crossing near Hwy 16, 13 Jul 1972, *A.M. Powell 244* (TEX); 21 km SW of Coyame on SE flank of Sierra de la Escondida, 29°22′N, 105°15′W, 22 Oct 1972, *Wendt, Chiang & Johnston 9814* (MO, LL); S and SE of Mina la Nueva Esperanza, E slope of Sierra del Morrión, 28°55′N, 105°21′W, 10 Jul 1972, *Chiang, Wendt & Johnston 8387* (LL); Santa Eulalia Mountains, 14 Aug 1885, *Pringle 369* (AA, F, GH, LL, MO – 2 sheets, NY – 2 sheets, US – 2 sheets); NW end of Sierra del Diablo, 29 – 30 Jul 1941, *Stewart 962* (F, LL, UC). **Coahuila**: SW flank of Sierra del Carmen, 29°04′N, 102°45′W, 15 Sep 1972, *Chiang, Wendt & Johnston 9278* (MO, LL); W Slope of Sierra del Jardín above (E of) Rancho El Caballo, 29°03′N, 102°38′W, 16 Sep 1972, *Chiang, Wendt & Johnston 9322* (LL); head of Cañón Ybarra, Sierra del Pino, 29 Aug 1941, *Stewart 1255* (F, GH, LL); Sierra del Pino, N of great cliffs about 10 mi N of Camp at La Noria, 22 Aug 1940, *I.M. Johnston & Muller 549* (GH, MICH, TEX); Crest of Sierra Planchada, N of Esmaralda, 25 Sep 1941, *I.M. Johnston 9392* (GH); Puerto de la Arena, Sierra Zacatosa, 7 km W of Zacatosa, 27°02′N, 102°48′W, 7 Aug 1973, *Chiang et al. 12100A* (LL); 2 km SW of Puertecito, W end of Sierra de la Madera, 21 Sep 1941, *I.M. Johnston 9313* (GH, LL); S part of Sierra de los Organos, 26°43′N, 103°01′W, 8 Aug 1973, *M.C. Johnston et al. 12125* (LL).

3d. Vauquelinia corymbosa subsp. **karwinskyi** (Maxim.) Hess & Henrickson comb. et stat. nov.

Vauquelinia karwinskyi Maxim. Trudy Imp. S.-Peterburgsk. Bot. Sada (Acta Horti. Petrop.) 6:236. 1879. Type: MÉXICO. Tamaulipas: Santyaguillo (Santiaguillo), Jun 1843, *Karwinsky 213* [lectotype: indicated by Standley (1922) as from Santiaguillo, here designated as specimen in upper left-hand corner of sheet as seen on photo at MOR! and TEX! from LE].

Vauquelinia potosina Painter ex Standl. Proc. Biol. Soc. Wash. 31:131. 1918. Type: MÉXICO. Luis Potosí Alvarez, 19 – 22 May 1905, *E. Palmer 594* (holotype: US!; isotypes: F! LL! MO – 2 sheets!).

Erect small trees with rounded to ovoid crowns to multi-stemmed shrubs 2 – 6(– 8) m tall; young stems initially tomentulose with crinkled hairs,

soon or occasionally tardily glabrate and puberulent. Leaves erect-ascending; leaf blades oblong-lanceolate, oblong-elliptical, oblong, oblong-ovate to ovate, rarely linear, (3−)4−9(−13.2) cm long, [5.5−]10−25(−36) mm wide, [length-width ratio (1.8−)2.2−5(−7)[−14]], coriaceous to stiffly coriaceous, 0.26−3.5 mm thick, acute, obtuse to rounded, usually mucronate at tip, abruptly to gradually, obliquely cuneate to rounded at base, at margins weakly to strongly crisped, uniformly, occasionally coarsely serrate to partially doubly serrate with (7−)10−14(−17) serrations per 5 cm [(1−)2−3 per 1 cm], serrations ascending or divergent, acute-acuminate or reduced to low rounded crenulations, (0.2−)0.5−2.5(−5.5) mm long, sometimes barely expressed; lamina flat or slightly conduplicately rounded, green to yellow-green, glabrous with yellow midveins above, yellow-green, glabrous, rarely with accumulations of wax, with rounded, raised, yellowish or slightly reddish midvein beneath; petioles (5−)7−27(−34) mm long, [(0.09−)0.15−0.3(−0.4) times as long as leaf blades], 0.9−1.5 mm thick, narrowly winged in distal half, often with sessile glands along wings, usually reddish to maroon brown, glabrous or puberulent adaxially. Compound corymbs 2−6.5(−8) cm long, (3−)5−10.5 cm wide; lower peduncles 15−40 mm long; pedicels-peduncles glabrate or tardily glabrate and puberulent-floccose; upper bracts-bracteoles subulate, 1−4.5 mm long with glands on margins; hypanthia 1.5−2.0(−2.5) mm long, 2.2−3.0 mm wide to 4.5 mm wide in fruit, glabrate to tardily pubescent-floccose outside, glabrous inside except at base; sepals (1.2−)1.5−2.0 mm long, 1.5−2.0 mm wide, bluntly mucronate, glandular along margins, glabrate or variously tardily floccose outside, mostly villous to sericeous inside and along margins; petals broadly oblong-ovate, ovate, 3−4(−4.5) mm long, 1.8−3 mm wide, broadly clawed at base; filaments 2.7−4.5(−5.2) mm long; anthers 0.7−1 mm long, to 1.2 mm long wet; styles 1.6−2.2 mm long. Capsules 4.5−6 mm long, 3−4.5 mm wide; seeds 3.5−5 mm long, 1−1.2 mm wide; embryos 1.7−2.3 mm long, 0.7−1.2 mm wide. (figs. 13, 17).

Vauquelinia corymbosa subsp. *karwinskyi* is characterized by its generally oblong, oblong-lanceolate, oblong-ovate, oblong-elliptical, usually relatively thickened, erect, serrate, partially doubly serrated leaf blades borne on moderately short, thickened, often reddish petioles (fig. 17).

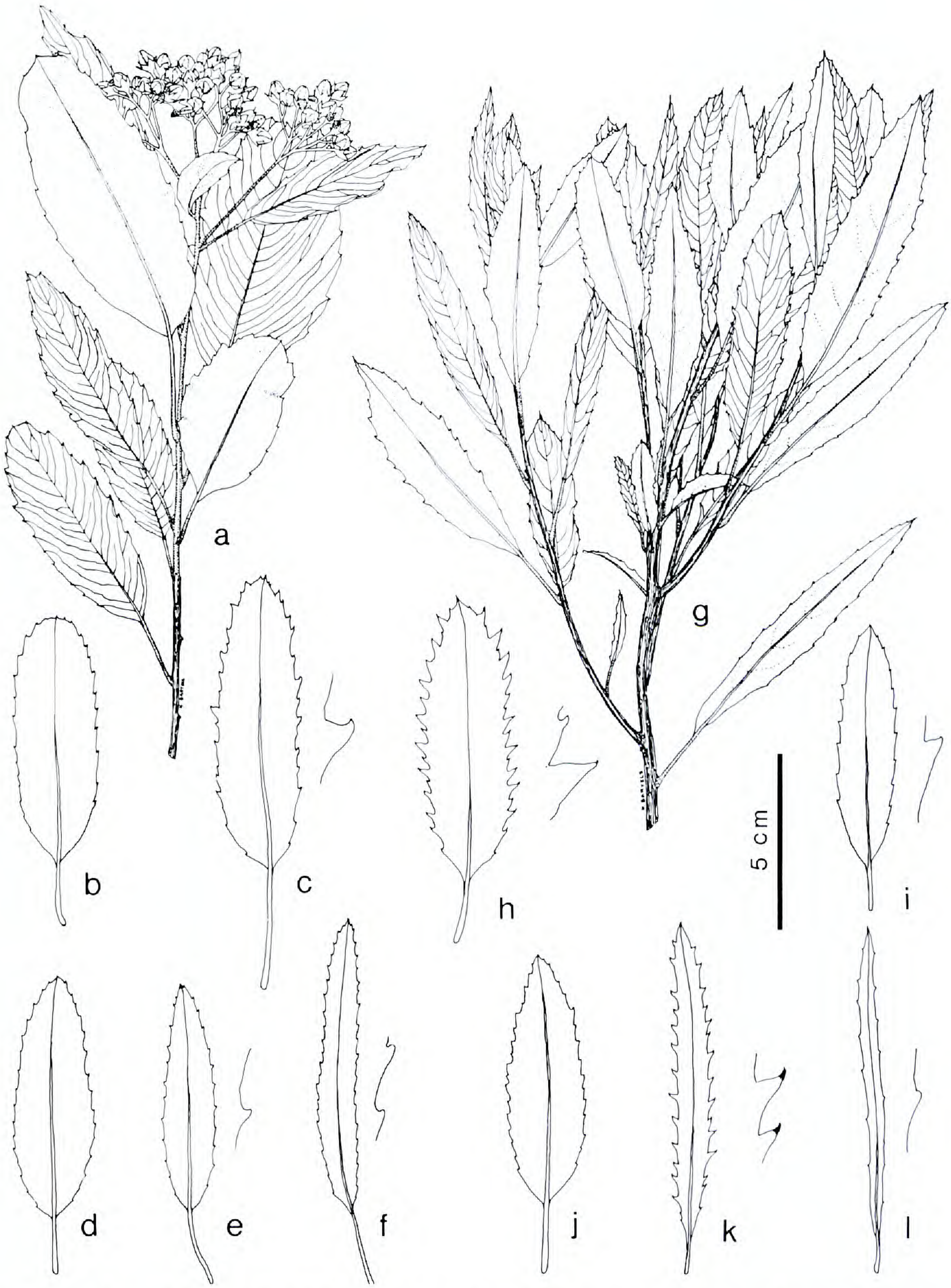
It differs from subsp. *corymbosa* by its much shorter, thicker petioles and more oblong, usually thicker leaf blades, from subsp. *heterodon* by its shorter leaf blades and petioles and by its much less pronounced serrations, from subsp. *saltilloensis* by its longer leaf blades and its tendency to have more glabrate inflorescences and stems, and from subsp. *latifolia*, with

which it is sometimes sympatric, by its narrower, non-glaucous leaf blades and its bushier, broader growth habit.

Vauquelinia corymbosa subsp. *karwinskyi* occurs along the western margin of the Sierra Madre Oriental with collections known from the state of San Luis Potosí east and northeast of Ciudad San Luis Potosí near San Francisco-Alvarez and near Guadalcazar and in Tamaulipas in the area around Miquihuana and Bustamente (fig. 13). In 1918, Standley named the San Luis Potosí populations *Vauquelinia potosina*, distinguishing them from those of the Tamaulipan *V. karwinskyi* on the basis of leaf morphology noting that the latter had broader leaves with more obtuse to truncate leaf bases. However, he later combined the two taxa in his *Trees and Shrubs of México* (Standley 1922). Some differences do exist between the San Luis Potosí and Tamaulipas populations. Those in San Luis Potosí tend to be taller trees with rounded crowns and single trunks and also tend to have slightly thinner leaf blades with more pronounced serrations and longer petioles, (11−)14−24(−31) mm long. In contrast, plants from Tamaulipas generally occur in more arid habitats, have a more ovoid, branched shrub to small tree habit, and tend to have thicker, more yellowish, somewhat conduplicately rounded leaf blades, with less pronounced marginal serrations and thicker, shorter petioles, (6−)9−17(−22) mm long. The leaf base and tip differences noted by Standley (1918) for erection of *V. potosina* are not consistent, as shown in representatives from a population collection by Hess & Byrne (*4642*, fig. 17b−f). It would be very difficult to define reliable differences between these population systems except for geography, as both populations are so variable in their leaf characteristics.

Occasional plants in Tamaulipas populations have much narrower leaf blades. A collection by González-Medrano *et al.* (*8672*) has linear leaf blades to 13 cm long and 5.5 mm wide, and in these characters is completely referable to *V. c.* subsp. *angustifolia*. Our collections from this region revealed an additional narrow-leaved collection (*Henrickson & Hess 19236*, fig. 17l) and an adjacent series of intermediate collections with broader, oblong-lanceolate, strongly serrate leaves (*Henrickson & Hess*

Fig. 17. *Vauquelinia corymbosa* subsp. *karwinskyi*. a-f.—Variation in leaf structure from collections from mountains E of Cd. San Luis Potosí. a.—Young stem showing leaves and inflorescence. Note variation in leaves. From collection 35 mi E of Cd. San Luis Potosí. *Hess & Byrne 4642*. b-f.—Leaf outlines showing variation in leaf shape, serrations, and petiole length from a population collection 20 mi E of Cd. San Luis Potosí. *Hess & Byrne 4631*. g-l.—Variation in leaf structure from collections from vicinity of Miquihuana, Tamaulipas. g.—Young stem showing narrow, erect-ascending, relatively thickened leaves. *Hess & Wilhelm 4357*. h-l.—leaf outlines showing extreme variation in leaf shape, serrations and petiole length from various collections. h-i.—Variation of one population in leaf shape and serration. *Henrickson & Hess 19094*. j.—Leaf outline from *Johnston, Chiang & Wendt 11176*. k-l.—A



local stand ca 10 km NW of Miquihuana has large individuals with abnormally narrow leaves. k.—*Henrickson & Hess 19240*. l.—This plant has leaves referable to *V. c.* subsp. *angustifolia*, but habit of plant and other features cause it to be referred to this taxon. *Henrickson & Hess 19236*. Magnifications as indicated, vertical bar = 1 cm for leaf margin enlargements.

19238, 19240, fig. 17k; see also *González-Medrano et al. 8672*) that approaches subsp. *heterodon* in leaf outline and serrations, though it lacks the long petiole characteristic of that taxon. Whether these narrow-leaved individuals represent true subsp. *angustifolia* brought in by long-distance dispersal or isolated here in post-pluvial times, or merely represent autochthonous extremes in variations of subsp. *karwinskyi* can only be resolved by further studies. As the leaves approach the texture of subsp. *karwinskyi* and the inflorescence and hypanthium are quite glabrous and lustrous, we here include these plants within the range of variation of subsp. *karwinskyi* until further evidence is obtained. Clearly the subsp. *heterodon*-like individuals with their shorter petioles and lack of consistent secondary serrations need not be referred to subsp. *heterodon*.

Vauquelinia corymbosa subsp. *karwinskyi* occurs in semi-arid limestone slopes from 1600 to 2300 m in association with species as *Juniperus flaccida, Pinus pinceana, P. nelsoni, Quercus pringlei, Q. rugosa, Rhus virens, Cornus excelsa, Prunus tetradenia, Juglans mollis, Helietta parvifolia, Forestiera reticulata, Yucca filifera, Agave lecheguilla* and species of *Dodonaea, Comarostaphylis, Cercocarpus, Lindleya, Cowania, Gochnatia, Garrya, Krameria, Dasylirion*, and *Nolina*.

Representative collections: MÉXICO. **San Luis Potosí**: 20 mi S of Huizache Jct. on Mex 54, 3 mi E on road to Guadalcazar, 22°42′N, 100°47′W, 14 Jun 1979, *Hess & Byrne 4705* (MOR); Cerro de San Cayetano, Guadalcazar, 23 Oct 1891, *P. Maury 7489* (NY[6]2 sheets); 20 mi E of San Luis Potosí on Mex 70, 22°04′N, 100°41′W, 5 Jun 1979, *Hess & Byrne 4631* (MOR); 35 mi E of San Luis Potosí, 8 mi E of San Francisco on Mex 70, 22°03′N, 100°32′W, 5 Jun 1979, *Hess & Byrne 4642* (MOR); Minas San Rafael, Jun 1911, *Purpus 5207* (F, GH, MEXU, MO, NY, UC, US). *Tamaulipas*: 12 km al N de La Perdida, Sierra de las Mulas, 20 Apr 1976, *González-Medrano et al. 8795* (MEXU); 15 km N de la Perdida, rumbo a Valle Hermoso, 16 Apr 1976, *González-Medrano et al. 8672* (CAS, MEXU, MO); 10 km NW of Miquihuana, along lower road to Marcela, 23°37′N, 99°52′W, 9 Oct 1982, *Henrickson & Hess 19238* (MOR, RSA); same area, date, *Henrickson & Hess 19240* (MOR, RSA); same area, date, *Henrickson & Hess 19236* (MOR, RSA); near town of Miquihuana, 23°42′N, 99°45′W, 8 Aug 1941, *Stanford, Retherford & Northcraft 780* (ARIZ, DS, GH, MO, NY, UC); 8 km by winding road N of Bustamente towards Miquihuana, 23°23′N, 99°51′W, 21 May 1973, *M.C. Johnston, Wendt & Chiang 11176* (LL); 14 km al SE de Palmillas, al W of Rancho "El Balcon", 24 Aug 1976, *González-Medrano, Sandoval C. & Zavaleta B. 9987* (MEXU, MICH).

3e. Vauquelinia corymbosa subsp. **saltilloensis** Hess & Henrickson subsp. nov.

A *Vauquelinia corymbosa* subsp. *karwinskyi* distincta laminis brevioribus pro parte (2.4 −)3 − 5(-raro 7) cm longis [non (3 −)5 − 9(− 13.2) cm longis] et petiolis brevioribus (4 −)5 − 11(− 14) mm longis [non (6 −)9 − 17(− 34) mm longis] et caule et inflorescentiae vestimento persistioribus, et statura abbreviore.

Multi-stemmed shrubs to small trees 1 − 2.5(− 4) m tall; young stems

moderately villous-canescent, persistently puberulent with short coiled hairs. Leaves erect-ascending, occasionally spreading; leaf blades variable in outline, ovate, elliptical to narrowly or broadly or oblong-ovate, or oblong-elliptical, (2.4−)3−6(−7) cm long, (10−)12−24(−33) mm wide, [length-width ratio (1.3−)1.7−3.2(−4.5)], coriaceous, 0.2−0.31 mm thick, acute to obtuse, occasionally irregularly retuse, mostly mucronate at tip, narrowly to broadly, often obliquely cuneate, more subrounded when broad at base, at margins plain or variously crisped, serrate, doubly serrate or partially doubly serrate with 2−5(−8) serrations per 1 cm, teeth ascending to divergent, 0.2−1.6 mm long, slender, acute-acuminate or low and blunt with sessile glands on inside margin at tip, often with sessile glands in axils of serrations and along margins between major serrations, these sometimes manifested as reduced secondary, slender, acuminate or blunt serrations; lamina green, lustrous, glabrate but usually persistently puberulent along yellow midvein above, yellow-green and similarly puberulent along raised, yellowish midveins beneath, occasionally glabrate throughout; petioles (4−)5−11(−14) mm long, [(0.1−)0.14−0.26(−0.3) times as long as leaf blades], moderately thick, 0.7−2 mm wide, winged by tapering leaf margins nearly to base, with sessile caducous glands along wings, usually persistly puberulent with slender, curled hairs to 0.1 mm long, at least on adaxial surface or throughout. Compound corymbs 2−4.5 cm long, 2.5−7 cm wide; basal peduncles 15−30 mm long; pedicels-peduncles initially tomentulose-villous with crisped hairs to 0.1−0.2 mm long, vestiture tending to persist as a close canescence into fruiting; upper bracts-bracteoles subulate, 1.2−2(−5) mm long, with sessile marginal glands; hypanthia 1.5−2 mm long, 1.7−2.5 mm wide, to 4 mm wide in fruit, sparsely puberulent outside, glabrous inside; sepals 1.3−1.5 mm long, 1.5−2 mm wide, thick, strongly mucronate, glandular along thin margins, puberulent to subglabrate outside, villous inside at tip and margins; petals oblong-ovate, oblong-obovate, 3.5−5 mm long, 2−3.2 mm wide, tapering to a broad claw at base; filaments 2.4−4.5 mm long; anthers 0.7−1 mm long; styles 1.3−2 mm long. Capsules 4−5 mm long, 3−4.3 mm wide; seeds 3.4−4.5 mm long, 1−1.2 mm wide; embryo 1.7−2.5 mm 0.7−0.9 mm wide.

TYPE: MÉXICO. COAHUILA: Cañón de San Lorenzo, 5−6 mi SE of Saltillo, lower cañón on dry rocky mountain sides, treelike, 4 m tall, flowers white, 28 May 1951, *R. McVaugh 12345* (HOLOTYPE: MICH!; ISOTYPE: US!). (figs. 13, 18).

Vauquelinia corymbosa subsp. *saltilloensis* is characterized by its variably narrowly to broadly ovate-elliptical, short-petiolate, often unevenly, coarsely doubly serrate, relatively short leaf blades and its tendency to have

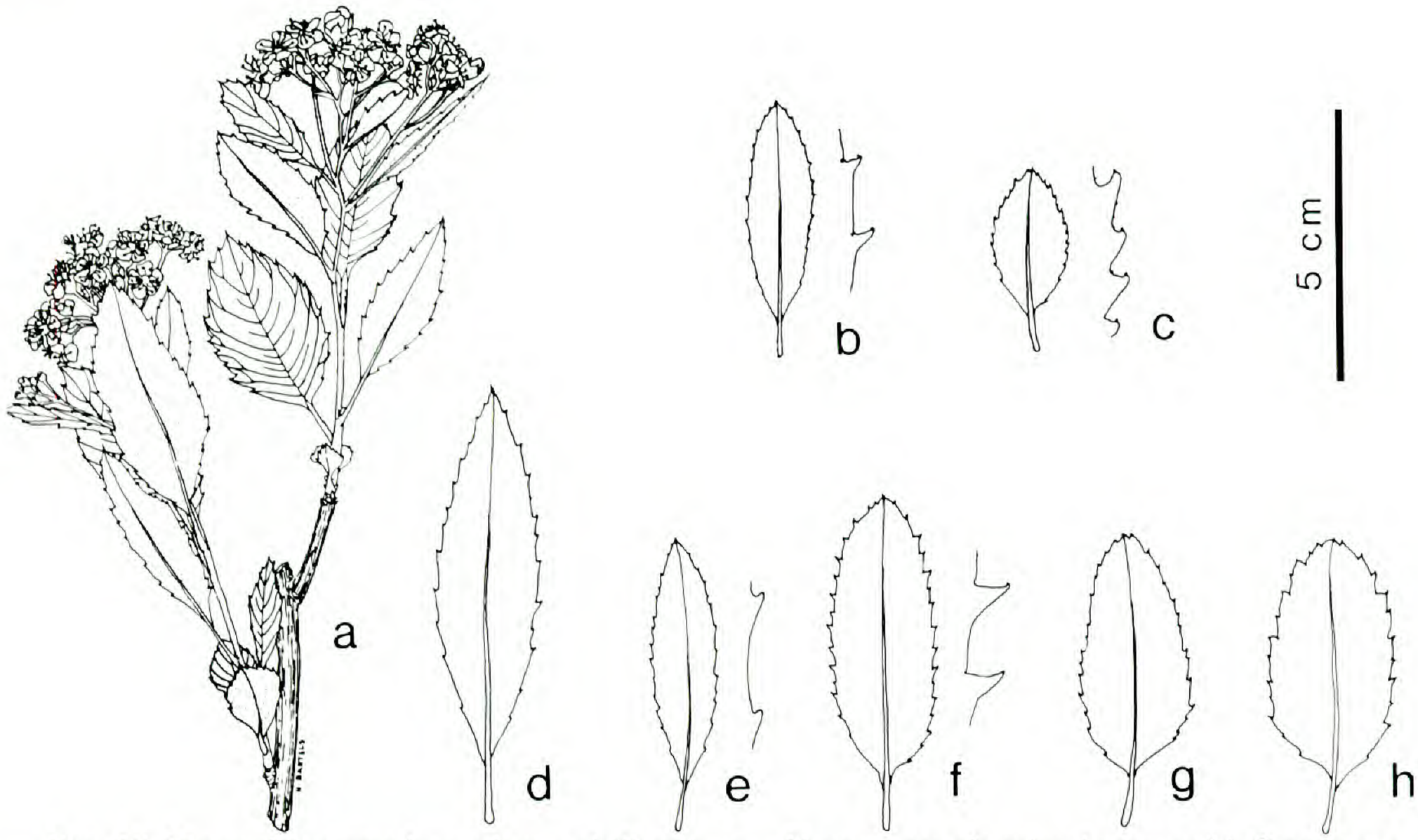


Fig. 18. *Vauquelinia corymbosa* subsp. *saltilloensis*. a.—Young stem showing leaves and inflorescence. Holotype from San Lorenzo Canyon, 5-6 mi SE of Saltillo, Coahuila. b-h.—Variation of leaf outline, serration, petioles, b.—From Saltillo area, *Hinton 18900*. c.—From near Galeana, Nuevo León. *Henrickson 18900*. e-h.—Variation in gathering from type locality in San Lorenzo Canyon, showing variation in outline and serration. *Hess & Wilhelm 4337*. Magnifications as indicated, vertical bar = 1 cm for leaf margin enlargements.

persistent hairs on the inflorescences, stems, petioles and along midveins on leaf blades and on the distinctly winged petioles (fig. 18).

The taxon is highly variable in leaf-blade shape, with some collections from the type locality having narrow- to oblong-ovate to nearly lanceolate leaf blades while other specimens have broadly oblong-ovate leaf blades (fig. 18d – h). Leaf margins are also variable, ranging from those uniformly once serrate with 5 – 8, slender, divergent serrations per 1 cm, as in *G.B. Hinton 16693* (US), to a more common type that is irregularly, often coarsely, doubly serrate with only 2 – 5 teeth per 1 cm (*Palmer 538, Henrickson 18900, Hess & Wilhelm 4337*, fig. 18b – h). As in other taxa serrations vary from prominent to very reduced, but they more often tend to be narrow.

In its coarse double serrations subsp. *saltilloensis* approaches subsp. *heterodon*, but subsp. *saltilloensis* has much shorter, broader leaf blades and shorter petioles and also tends to be more persistently pubescent on inflorescence, stems, petioles and midveins. Some specimens approach subsp. *corymbosa* in leaf shape, but they again have shorter, thicker petioles unlike that taxon. The new taxon is perhaps most similar to subsp. *karwinskyi*, which is also variable in leaf-blade shape and has similar short petioles, but subsp. *saltilloensis* has smaller leaves that more often tend to

be doubly serrate, and it is again more persistently pubescent. In its shorter petioles, the new taxon is more similar to the Tamaulipan populations of subsp. *karwinskyi* than to the San Luis Potosí specimens. Although the new taxon is highly variable, it is recognized as a distinct taxon mainly as it cannot easily be combined with any other taxon.

The new taxon occurs in mid-elevational hillsides from 1900 to 2200 m in southeastern Coahuila, with most collections from the limestone Cañón de San Lorenzo near Saltillo and from adjacent Nuevo León both from near Monterrey and near Galeana (fig. 13). It occurs in association with *Malacomeles, Acacia, Agave scabra, Baccharis, Berberis trifoliolata, Bouvardia, Comarostaphylis, Cercis, Cercocarpus, Dalea, Dasylirion, Fraxinus, Garrya, Juniperus flaccida, Lindleya, Nolina, Ptelea, Quercus, Rhus*, and *Salvia*, with an understory of *Stipa tenuissima*, and other species.

Additional collections: MÉXICO. **Coahuila**: San Lorenzo Canyon, 6 mi SE of Saltillo, 16 Apr 1905, *Palmer 538* (NY, US); Cañón de San Lorenzo, W-drainage canyon in Sierra de Pame, 5 mi due S of Saltillo, 25°20′N, 100°59′W, 23 Jul 1977, *Wendt & Valdez R. 2010* (TEX); near Saltillo, limestone hillside, 25 May 1947, *Hinton 16693* (US); 5 mi SE of Saltillo, ca 3 mi E of Mex Hwy 54, in Sierra de Poliname, 11 Jun 1978, *Hess & Wilhelm 4337* (MOR); ca 35 km E of Saltillo, road to La Carbonera, 15 – 20 km E of Hwy 57, 15 Aug 1974, *Spjut, Barclay & Sallee 4302* (CAS). **Nuevo León**: Sierra Madre Mts., Monterrey, 29 Jul 1933, *C.H. & M.T. Muller 541* (F, GH, MEXU, TEX); 5 km NNE of Galeana, 25 Apr 1982, *Henrickson 18900* (MOR).

3f. VAUQUELINIA CORYMBOSA subsp. **latifolia** (Rydb. ex Standl.) Hess & Henrickson comb. et stat. nov. *Vauquelinia latifolia* Rydb. ex Standl. Contr. U.S. Natl. Herb. 23(2):323. 1922. TYPE: MÉXICO. TAMAULIPAS: Mountains near Miquihuana, shrub 4 – 8 ft, white fl., 10 Jun 1898, *E.W. Nelson 4481* (HOLOTYPE: US!; ISOTYPES: F!, GH!, NY!).

Multi-stemmed, often slender, spindly, erect shrubs (1 –)2 – 4(– 5) m tall; young stems glabrate-glabrous, dark reddish, glaucous, thick, to 2 – 4(– 5) mm in diameter. Leaves erect-ascending, occasionally spreading; leaf blades variable in outline, ovate-lanceolate, ovate, oblong to oblong-ovate, broadly ovate, rarely nearly orbicular, (3 –)5 – 8(– 12.5) cm long, (15 –)25 – 45(– 65) mm wide, [length-width ratio (1.1 –)1.4 – 2.7(– 3.4)], stiffly coriaceous, 0.27 – 0.43 mm thick, acute, obtuse, to nearly rounded, occasionally retuse, usually distinctly mucronate at tips, broadly, obliquely cuneate, truncate, rounded or, when very broad, subcordate at base, at margins strongly to weakly crisped, often coarsely, sharply serrate or partially doubly serrate with 8 – 14(– 24) serrations per 5 cm [(1 –)2 – 5 per 1 cm], serrations ascending to divergent, acute-acuminate, apiculate, (0.8 –)1.2 – 4.5(– 6.5) mm long, rarely margins partially or completely entire, serrations only rarely with sessile glands in axils or at tip; lamina flat or variously conduplicate,

yellow-green, glabrous, glaucous with midvein yellow to dull red above, more yellow green, bluish-glaucous with midvein raised, yellowish to dull red beneath; petioles (7−)10−18(−21) mm long [0.14−0.22 (−0.28)[−0.37] times as long as leaf-blade], thick, 1.2−2.5 mm in diameter, neither winged nor glandular along margins, glabrous, glaucous, dull reddish. Compound corymbs 5−10 cm long and wide; lower peduncles 12−55 mm long; pedicels-peduncles glabrate to glabrous; upper bracts-bracteoles subulate, 1−5.5 mm long, without glands on margins; hypanthia 1.5−2.5 mm long, 2.5−3 mm wide, to 5.5 mm wide in fruit, glabrous outside, glabrous inside but sericeous near ovary at base; sepals 1.5−2 mm long, 1.4−2 mm wide, thick, bluntly mucronate at tip, glabrous to floccose outside, glabrous or nearly so or slightly sericeous in mid-portion or marginally villous inside, marginal glands lacking; petals oblong-ovate, 3.5−4.5 mm long, 2−3.3 mm wide, broadly clawed at base; filaments 2.7−4.5 mm long; anthers 0.7−1.0 mm long, to 1.2 mm long wet; styles 1.7−2 mm long. Capsules 4.5−7 mm long, 4−5.5 mm wide; mature seeds and embryos not seen (figs. 13, 19).

Vauquelinia corymbosa subsp. *latifolia* is one of the more distinctive subspecies of *V. corymbosa*, distinguished by its erect, slender, often rather sparse, sucker-shoot-like growth habit with relatively thickened, erect, long-shoot stems 2−4(−5) mm in diameter. Leaves are thick, stiffly coriaceous, glabrous, glaucous, usually large, ovate, broadly ovate, sometimes narrowly ovate with coarsely serrate, crisped margins borne on relatively short, thick, dark red-maroon, glaucous petioles (fig. 19). Unlike other subspecies leaf margins do not extend down the petioles as wings, serrations do not terminate in distinct glands, and only rarely are sessile, caducous glands produced in their axils. When leaf blades are broad, they are often broadly rounded-truncate to slightly cordate at the base. Flowers also tend to have oblong-ovate, shortly clawed petals and more glabrate inner sepal surfaces.

The subspecies is often sympatric with the more densely-branched, bushy subsp. *karwinskyi*, which also tends to have red-maroon petioles and thicker, though smaller leaves—characteristics that tend to indicate introgression between the two taxa. It is admittedly sometimes difficult to assign incomplete herbarium specimens with smaller leaves to either taxon, but separation is much easier in the field, for subsp. *latifolia* often produces what appears to be elongate, erect, sucker shoots with their characteristic, very thick, glaucous leaves.

Vauquelinia corymbosa subsp. *latifolia* occurs on limestone slopes in xeric chaparral in northwestern Tamaulipas in the Miquihuana area (fig. 13)

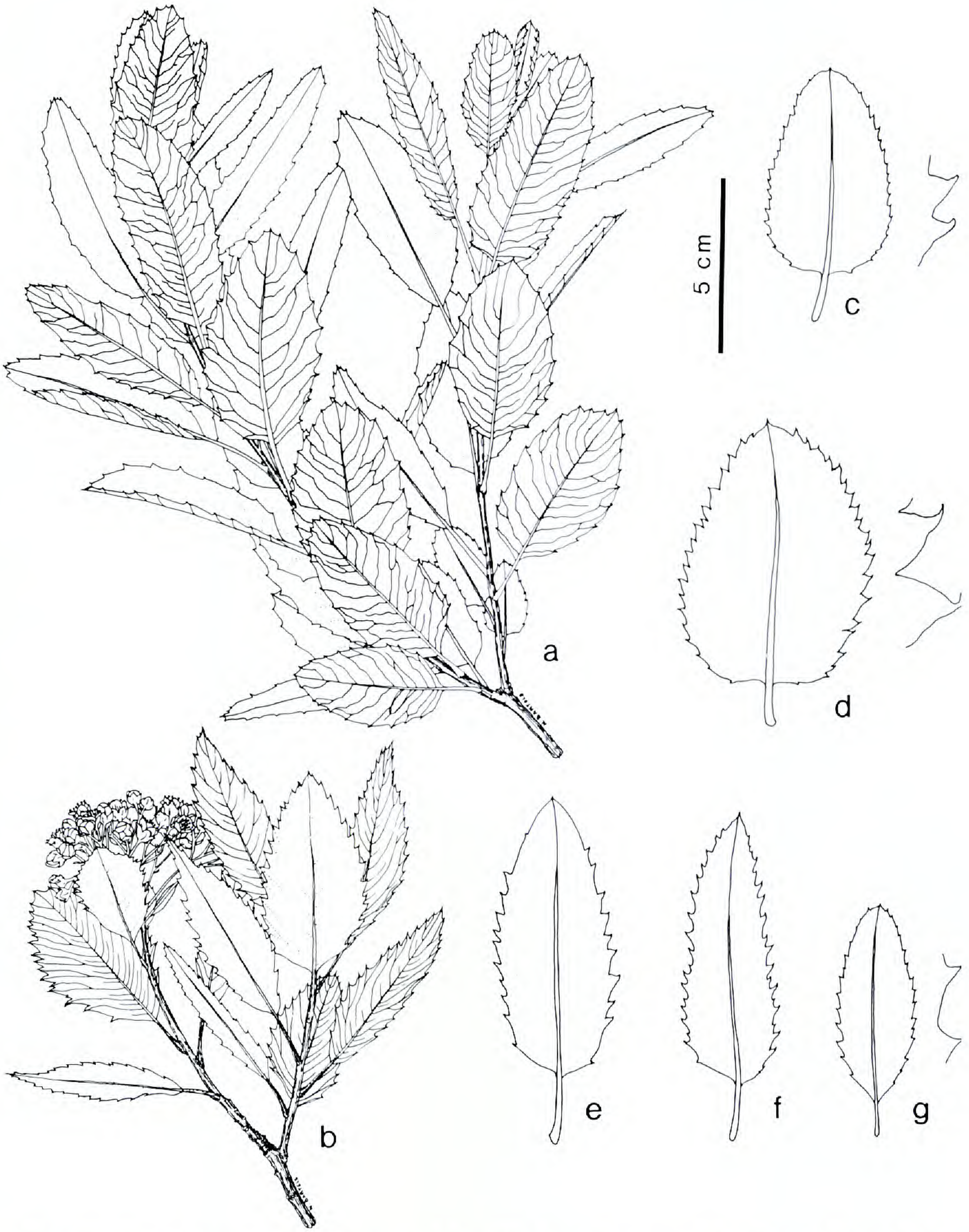


Fig. 19. *Vauquelinia corymbosa* subsp. *latifolia*. All plants from near Miquihuana, Nuevo León. a.-b.—Young stems with characteristic ovate leaves. Note differences in marginal toothing. The characterisitc leaf thickness is not demonstrated in the illustrations. a.—*Henrickson & Hess 19235*. b.—*Hess & Byrne 4713*. c-f.—Leaf outlines showing shape, marginal serrations, and petiole lengths. c.—Leaf from isotype. *Nelson 4481*. d-e.—Variation from a population collection. *Henrickson & Hess 19210*. f-g.—Variation from a population collection. *Henrickson & Hess 19151*. Magnifications as indicated, vertical bar = 1 cm for leaf margin enlargements.

from 1700 to 2400 m in association with *Cercocarpus fothergilloides*, *Rhus virens*, *Agave lecheguilla*, *Hechtia scariosa*, *Berberis gracilis*, *Quercus pringlei*, *Ceanothus greggii*, *Leucophyllum zygophyllum* and species of *Mortonia*, *Litsea*, *Lindleya*, *Gochnatia*, *Dasylirion*, *Dodonaea*, and *Salvia*.

Representative collections: MÉXICO. **Tamaulipas**: Between Hermosa and Miquihuana, 23 Jul 1949, *Stanford, Lauber & Taylor 2684* (NY, US); Cañada de Joya de Gomez, 25 km al NE de al Peña, 26 May 1974, *González-Medrano et al. 7131* (MEXU); 8 km N de la Perdida, 15 Apr 1976, *González-Medrano et al. 8643* (MEXU); Llano del Milagro, 8 km al N de Valle Hermosa, 17 Apr 1976, *González-Medrano et al. 8711* (CAS, MEXU, MO); 10 km NW of Miquihuana, along lower road to Marcela, 23°37′N, 99°52′W, 9 Oct 1982, *Henrickson & Hess 19235* (MOR, TEX); ca 14 km NW of Miquihuana, ca 20 km N of La Perdida towards Marcela, 23°40′N, 99°47′W, 9 Oct 1982, *Henrickson & Hess 19210* (MOR, TEX).

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THE GENUS *ERIOCHLOA* (POACEAE: PANICEAE) IN NORTH AND CENTRAL AMERICA

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ABSTRACT

Eriochloa is a genus of the grass tribe Paniceae, with a base chromosome number of $x = 9$. Most species are tetraploids ($2n = 36$); however, diploids ($2n = 18$), hexaploids ($2n = 54$) and octoploids ($2n = 72$) have been reported. The first chromosome count for *E. michauxii* is reported ($2n = 36$). The genus is represented in North and Central America by eight perennial and seven annual species which are predominantly distributed in the southwestern U.S. and Mexico. Keys and descriptions were produced using the DELTA computer programs. Distributions and representative specimens are provided for all taxa. The binomial *E. acuminata* was found to have priority over *E. gracilis*, and the new combination *E. acuminata* var. *minor* (Vasey) R.B. Shaw was required. Two taxa are reduced to varietal rank with the new combinations *E. aristata* var. *boxiana* (Hitchc.) R.B. Shaw and *E. setosa* var. *ekmanii* (Hitchc.) R.B. Shaw presented. The occurrence of *E. pseudoacrotricha*, an Australian species, is reported for the first time in North America. The name *E. fatmensis* is applied to specimens previously identified as *E. procera*.

INTRODUCTION

Eriochloa Kunth occurs throughout the tropical, subtropical and warm-temperate regions of the world. Fifteen species occur in North and Central America and the West Indies. Four taxa [*E. fatmensis* (Hochst. & Steud.) W.D. Clayton, *E. pacifica* Mez., *E. pseudoacrotricha* (Stapf ex Thell.) C.E. Hubb., *E. villosa* (Thunb.) Kunth] are either introduced or adventive in the area and may not be permanent members of the flora. *Eriochloa distachya* Kunth, predominately a South American species, reaches its northern limits in Guatemala. *Eriochloa setosa* (A. Rich.) Hitchc. is endemic to Cuba, while *E. michauxii* (Poir.) Hitchc. is found only in Florida and Georgia. The most widely distributed taxon of *Eriochloa* in the western hemisphere is *E. punctata* (L.) Desv. ex Hamilt. which occurs throughout the Gulf Coast regions of the U.S., Mexico, the West Indies and extends

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into Central and South America. The major area of diversification of the genus in North America is in the southwestern U.S. and Mexico, where five annual and one perennial species occur. The perennial, *E. sericea* (Scheele) Munro ex Vasey, is found throughout Texas grasslands and extends into southern Oklahoma and northern Coahuila, Mexico. The annuals [*E. acuminata* (Presl) Kunth, *E. aristata* Vasey, *E. contracta* Hitchc., *E. lemmonii* Vasey & Scribner, *E. nelsonii* Scribner & Smith] are a group of weedy, taxonomically difficult species found throughout the region.

Economically, the genus has limited value as forage plants. *Eriochloa sericea* is the only native perennial abundant enough to be considered an important forage species. It occurs as a climax dominant decreaser on the Edwards Plateau of Texas where it is a high quality cattle forage (Shaw & Smeins 1983). *Eriochloa polystachya* Kunth is used as a pasture grass in the Caribbean and South America (Judd 1975); however, attempts to establish this species in the U.S. has had limited success. The annuals *E. acuminata* and *E. contracta* are noxious weeds in the southwestern U.S., and their infestation of field crops presents a problem.

Shaw & Smeins (1981) concluded that the genus is properly placed in the Paniceae. Typical panicoid features of the leaf blade epidermis include bicellular microhair shape, silica-body shape, subsidiary cell shape and intercostal and costal zone cellular arrangement. The leaf blade anatomy in cross-section is indicative of C_4 panicoid grasses, as are the carbon isotope ratios (Shaw & Smeins 1981). *Eriochloa* along with *Brachiaria* (including *Pseudobrachiaria*), *Urochloa* and one species of *Panicum* (*P. maximum* Jacq.) are the only members of the Paniceae which utilize the PEP decarboxylating enzyme (Gutierrez, et al. 1976).

Significant diagnostic characteristics of *Eriochloa* include the absence of bristles (i.e., the spikelet bearing branches terminate in a spikelet), a paniculate inflorescence with racemose primary branches, the rachilla not pronounced between the florets, a glabrous upper lemma, disarticulation at the spikelet base, the transversely rugose upper floret, and typical absence of the first glume. *Eriochloa* is distinguished from all other members of the Paniceae by the fusion of the first glume and callus to form a cup-like structure at the spikelet base. Clayton (1975) briefly discussed the relationship between *Eriochloa* and *Brachiaria* and drew attention to *B. callopus* (Pilg.) Stapf, which has a bead-like swelling at the spikelet base. Clayton (1980) later transferred this species to *Echinochloa* and indicated that *Echinochloa* and *Brachiaria* were difficult to separate. Our studies showed that *Echinochloa callopus* (Pilg.) W.D. Clayton is not related to *Eriochloa*. It has a well-formed first glume, the swelling at the base of the spikelet appears structurally different from the *Eriochloa* cup, the nerves of

the second glume and lower lemma are distinctly spiculate, the upper floret is smooth, the apex of the upper lemma is differentiated into a green membranous area which is typical of *Echinochloa*, and the apex of the upper palea is reflexed. *Echinochloa* is easily distinguished and not closely related to *Brachiaria, Eriochloa* or *Urochloa*.

Based on the presence of bicellular microhairs, silica-bodies and interlocking long cells on the epidermis of the callus, Shaw & Smeins (1979) concluded that the callus is at least in part a remnant of the first glume. A rudimentary first glume is consistently found in *E. polystachya, E. rovumensis* (Pilg.) W.D. Clayton and *E. meyerana* (Nees) Pilg. (Clayton 1975; Shaw & Smeins 1984) and rarely in spikelets of *E. contracta* and *E. michauxii*. Shaw & Smieins (1984) concluded that the callus is a unique structure consisting of swollen internode tissue between the pedicel and spikelet and not totally composed of first glume remnants.

Cytologically, the genus has a base chromosome number of $x=9$. A majority of species in North and Central America are tetraploids ($2n=36$). The annual tetraploid taxa frequently overlap in morphological characteristics when they are sympatric, which implies hybridization among these species. This perceived ability to hybridize may explain the tendency of some taxonomists to follow Gould (1950) and group several taxa into a single polymorphic species. Two diploid ($2n=18$) and two hexaploid ($2n=54$) species have been reported. An octoploid ($2n=72$) chromosome number has been found for *E. nelsonii* var. *papillosa* R.B. Shaw. (John Reeder, pers. comm.). The tetraploid number ($2n=36$) for the perennial *E. michauxii* var. *michauxii* is the first report for this taxon.

The taxonomy and nomenclature of *Eriochloa* has been relatively stable due to the early use of the callus as a diagnostic feature of the genus. The generic name *Eriochloa* was first published by Kunth in 1816. The name is from the Latin *erion* meaning woolly and *chloa* meaning grass, which refers to the densely pubescent pedicels and spikelets of the type species *E. distachya*.

Four years prior to the publication of *Eriochloa* by Kunth, Palisot de Beauvois in 1812 published the generic name *Monachne*. The basis for this name was the description (as translated by Niles & Chase 1925): "Inflorescence paniculate; panicle compound; glumes subequal, villous, longer than the floret, lower floret staminate, the lemma membranaceous, hyaline, the palea wanting; upper floret perfect, the lemma coriaceous-indurate, entire." Palisot de Beauvois did not indicate a type species but related the genus to two species, *M. racemosa* and *M. unilateralis*. Based on the drawing of *M. racemosa*, this species appears allied to *Panicum urvilleanum* Kunth. *Monachne unilateralis* as figured is undoubtedly an

Eriochloa because of the obvious callus at the base of the spikelet but has not been equated to any known species. Thus, Palisot de Beauvois based the concept of *Monachne* on two discordant elements.

Nash (1903) accepted the generic name *Monachne* when describing the species *M. subglabra* (= *E. polystachya*), but later used the name *Eriochloa* and listed *M. unilateralis* as a tentative synonym of *E. michauxii* (Nash, 1912). Hitchcock (1908) did not find sufficient evidence for accepting *Monachne* in place of *Eriochloa*. He believed *M. unilateralis* had no description and could not be identified from the figure. Niles and Chase (1925) solved the problem by lectotypifying *Monachne* with *M. racemosa* as the type, thus synonymizing *Monachne* into *Panicum*.

METHODS

This revision is based on data collected in a detailed study of populations and specimens of *Eriochloa* in North and Central America. For a detailed discussion of justification for nomenclatural changes see Shaw (1979). To insure uniformity and standardization the key and descriptions were produced from the DELTA taxonomic programs (Dallwitz 1978, 1980 & 1984). Advantages and methods for the application of these programs in revisions and floras at the species level are given in Webster (1984, 1986a & 1986b). Application of the DELTA programs at the generic level was pioneered by Watson (cf. Watson & Dallwitz 1985; Watson, et al. 1986a; Watson et al. 1986b).

TAXONOMY

ERIOCHLOA Kunth, Nov. Gen. Sp. 1:94. 1816. TYPE: *Eriochloa distachya* Kunth

Monachne, auct. non Beauv. (Ess. Agrostogr. 49. 1812), *p.p. maj. excl. typ.*
Helopus Trin., Fund. Agrost. 103. 1820.
Oedipachne Link, Hort. Berol. 1:51. 1827.
Aglycia Willd. ex Steud., Nom. Bot. 2(1):37. 1840.

Plants hermaphroditic; annual, or perennial. Flowering culms woody, or not woody; caespitose, or not caespitose; erect, or decumbent; terminated by a solitary inflorescence. Nodes hairy, or glabrous. Internodes hollow. Leaves not obviously differentiated; not distinctly distichous; without auricles. Sheaths rounded, or laterally compressed; the margins not fused. Ligule a ciliate membrane, or a fringe of hairs (usually a fringe of hairs with a minute membranous rim at the base). Leaf blades linear to lanceolate; flat to involute; the base cuneate to rounded; not awned. Inflorescence a panicle; fully exserted at maturity, or partially enclosed in the

leaf sheath. Main axis present. Primary branches with secund spikelets; with appressed secondary branches. Rachis terminating in a spikelet. Pedicels present; discoid; concave. Disarticulation at the spikelet base. Callus differentiated; not prolonged into a stipe; not flared to form a discoid receptacle; glabrous. Cleistogamous spikelets absent. Spikelets solitary, or paired; all pedicellate; homomorphic; not embedded in the rachis; adaxial. First glume present, or absent (typically completely reduced); fused with the callus to form a cup-like structure. Rachilla pronounced below the second glume; not pronounced between the florets; straight; not twisted; filiform; lacking lateral appendages; terminating in well-formed floret. Second glume present; 1 to 1.4 × the length of the lower floret; not saccate; convex; glabrous, or hairy; indumentum not uncinate; muticous to awned. Sterile floret staminate, or lacking stamens. Lemma of sterile floret without a hyaline area at the base; muticous, mucronate, or awned. Palea of sterile floret fully developed, or vestigial, or absent. Lemma of fertile floret rugose; dull; with involute margins; glabrous; the nerves not pronounced; rounded on the back; the margins not thinner in texture than the body. Germination flap conspicuous. Palea of fertile floret well-developed; not splitting at maturity. Lodicules present; not fused; glabrous. Anthers lacking an apical tuft of hairs. Caryopsis not longitudinally grooved. Endosperm solid. Styles not persistent; not fused.

KEY TO THE SPECIES

1(0). Lemma of fertile floret muticous or with a mucro less than 0.2 mm long, second glume not awned 2
Lemma of fertile floret with an awn greater than 0.2 mm long or with an awned second glume 10

2(1). Spikelets solitary 3
Spikelets paired at the mid-point of the primary branches 6

3(2). Spikelets less than 2.0 mm wide; perennial 4
Spikelets 2 − 2.5 mm wide; annual . . . . . *E. villosa*

4(3). Primary branches of the inflorescence 1 − 2, rarely 3 − 4; spikelets divergent from the rachis . . . . . *E. distachya*
Primary branches of the inflorescence usually more than 3; spikelets not distinctly divergent from the rachis 5

5(4). Apex of the pedicels with a corona of long straight hairs; leaf blades less than 5 mm wide, usually involute; primary branches of the inflorescence appressed to the main axis, with neatly arranged spikelets; palea of sterile floret absent . . . . . *E. sericea*
Apex of the pedicels without a corona of long straight hairs; leaf blades more than 5 mm wide, usually flat; primary branches of the inflorescence spreading from the main axis, with loosely arranged spikelets; palea of the sterile floret present . . . . . *E. michauxii*

6(2). Annual 7
Perennial 9

7(6). Spikelets divergent from the rachis, neatly arranged on the primary branches; lower lemma hairy on the lower 1/2 – 2/3 and glabrous above; spikelets 5 – 8 mm long . . . . . *E. nelsonii*
Spikelets not distinctly divergent from the rachis, loosely arranged on the primary branches; lower lemma not hairy and glabrous; spikelets less than 5 mm long 8

8(7). Leaf blades with velvety pubescence; leaf blades lanceolate; palea of the lower floret present; internodes densely hairy . . . . . *E. lemmonii*
Leaf blades glabrous or with scattered short hairs, not velvety; leaf blades linear; palea of the lower floret absent; internodes glabrous or with a few scattered hairs . . . . . *E. acuminata*

9(6). Spikelets 3.2 – 3.9 mm long; first glume present; flowering culms decumbent, rooting at the lower nodes . . . . . *E. polystachya*
Spikelets greater than 3.9 mm long; first glume absent; flowering culms erect, not rooting at the lower nodes . . . . . *E. michauxii*

10(1). Apex of pedicels with a corona of long straight hairs 11
Apex of pedicels lacking a corona of long straight hairs 12

11(10). Annual; primary branches of the inflorescence hairy; second glume not awned; inflorescence with a hairy main axis, the primary branches not winged . . . . . *E. pacifica*
Perennial; primary branches of the inflorescence glabrous; second glume awned; inflorescence with a glabrous main axis, the primary branches winged . . . . . *E. pseudoacrotricha*

12(10). Spikelets solitary 13
Spikelets paired at the mid-point of the primary branches. 15

13(12). Annual; leaf blades linear, usually flat, more than 2.0 mm wide; main axis of the inflorescence more than 40 mm long 14
Perennial; leaf blades filiform, involute, less than 2.0 mm wide; main axis of the inflorescence less than 40 mm long . . . . . *E. setosa*

14(13). Primary branches of the inflorescence spreading at maturity, 0.4 – 0.6 mm wide, glabrous, with loosely arranged spikelets; nodes glabrous . . . . . *E. fatmensis*
Primary branches of the inflorescence contracted at maturity, less than 0.4 mm wide, hairy (scattered short straight hairs), with neatly arranged spikelets; nodes pubescent . . . . . *E. contracta*

15(12). Spikelets less than 3.5 mm long . . . . . *E. fatmensis*
Spikelets greater than 3.5 mm long 16

16(15). Annual; primary branches hairy; second glume awned; pedicels hairy; lacking rhizomes . . . . . *E. aristata*
Perennial; primary branches glabrous; second glume muticous to apiculate; pedicels glabrous; rhizomatous . . . . . *E. punctata*

ERIOCHLOA ACUMINATA (Presl) Kunth, Rev. Gram. 1: Suppl. 8. 1830.

Piptatherum acuminatum Presl, Reliq. Haenk. 1:221. 1830. TYPE: MEXICO. Hab. in Mexico (HOLOTYPE: fragment K!).

Plants annual. Cataphylls absent. Flowering culms 3 – 12 dm tall; erect,

or decumbent; rooting or not rooting at the lower nodes; 2 – 5-noded. Nodes hairy, or glabrous. Internodes glabrous. Sheaths not overlapping; conspicuously inflated, or not inflated; chartaceous; 40 – 80 mm long; glabrous, or hairy; pubescent. Ligule a fringe of hairs; 0.2 – 1.2 mm long. Leaf blades linear; flat; straight to flexuous; spreading; 5 – 12 cm long (– 18); 5 – 12 mm wide (2 – 16); adaxially smooth; glabrous, or hairy on the adaxial surface. Prophyllum 40 – 70 mm long. Peduncle 120 – 260 mm long; hairy. Inflorescence 10 – 60 mm wide. Main axis 70 – 160 mm long; scabrous, or hairy. Primary branches appressed to the main axis to spreading; 5 – 20 on the main axis (– 30); 10 – 50 mm long; 0.4 – 0.6 mm wide; not winged; hairy; pubescent to setose; with loosely arranged spikelets. Pedicels 0.1 – 1 mm long; hairy; with hairy or glabrous apices. Spikelets 20 – 36 on a typical primary branch; paired (becoming solitary towards the apex); not divergent from the axis; lanceolate to ovate; 3.8 – 5 mm long (– 5.5); 1.1 – 1.4 mm wide. First glume absent. Second glume 1 × the length of the lower floret; lanceolate to ovate; 5-nerved; hairy; acuminate to acute; mucronate to awned. Second glume awn 0 – 1.2 mm long. Sterile floret lacking stamens. Lemma of the sterile floret lanceolate to ovate; 3.6 – 5 mm long; 1.1 – 1.4 mm wide; 5-nerved (rarely 7); the surface hairy; setose; acuminate to acute; muticous. Palea of sterile floret absent. Fertile floret 0.7 – 0.9 × the length of the sterile floret. Lemma of fertile floret elliptic; 2.3 – 3.3 mm long; 5-nerved; rounded, mucronate (the mucro 0.1 – 0.3 mm long). Chromosome number $2n = 36$ for var. *acuminata* (Gould 1966; *Shaw 1078*) and var. *minor (Shaw 1091)*.

KEY TO THE VARIETIES OF ACUMINATA

Spikelets long-acuminate or tapering to a short awn, 4 – 6 mm long; leaf blades usually glabrous but occasionally pubescent ..... var. *acuminata*

Spikelets acute, generally less than 4 mm long; leaf blades usually pubescent but occasionally glabrous ..... var. *minor*

ERIOCHLOA ACUMINATA var. ACUMINATA. Fig. 1.

Helopus gracilis Fourn., Mex. Pl. 2:13. 1886. *Eriochloa gracilis* (Fourn.) Hitchc., J. Wash. Acad. Sci. 23:455. 1933. *Eriochloa lemmonii* Vasey & Scribner var. *gracilis* (Fourn.) Gould, Leafl. West. Bot. 6:51. 1950.

Habitat and distribution: Often growing as a weed in ditches, fields, road right-of-ways, and other disturbed areas, common throughout the southwestern United States and most of Mexico, and becoming established and spreading throughout the southeastern U.S.

Representative specimens: MEXICO. **Baja California Sur**: 1 mi N of Triumfo, *Gould 12142a* (ENCB, MICH); Sierra de la Giganta, *Carter & Moran 5369* (ENCB); 4 mi S of El

Pescador, *Reeder & Reeder 5677* (ENCB); 6 – 8 mi N from Cuarenta, *Thomas 8348* (ENCB). **Chihuahua**: 20 km S of Camargo, *Harvey 1385* (MO); Sierra de los Organos, *LeSueur 0171* (US); bank of Conchos River, *Pilsbry 19325* (NY); 5 mi N of Parral, *Reeder, Reeder & Goodding 1687* (ENCB); 4 mi E of Cd. Delicias, *Reeder, Reeder & Goodding 1258* (ENCB); 80 km al N de Chihuahua, Torreon, *Palmer 509* (F). **Durango**: Gomez Palacio, *Beetle M-1856* (TAES); 14 mi SE of Durango, *Gould 12290* (TAES); Durango, *Palmer 736* (MO, TAES); 3 mi N of Las Nieves, *Reeder, Reeder & Goodding 1679* (ENCB). **Guanajuato**: 10 km al E de Yuriria, *Rzedowski 27614* (ENCB, MICH). **Jalisco**: 3 km NW of Villa Corona, *McVaugh 19454* (NY); 2 mi W of San Miguel, *Reeder & Reeder 6382* (ENCB, US). **Michoacan**: Morelia, *Arsene 5644* (MO); S of Lake Cuitzeo, *Sohns 730* (TAES). **Morelos**: 16 km SE de Cuautla, *Becerra NB-39-75* (ENCB); 10 mi S of Guernavaca, *Gould 9573* (TAES). **Puebla**: 3.5 mi E of Jct. of Hwy 190 and 160, *Torke, Dunn & Ellis 351* (ENCB); Tepexco, *Rzedowski 20489A* (TAES). **Queretaro**: 6 mi SE of Queretaro, *Reeder & Reeder 2974* (ENCB); 5 mi N of Queretaro, *Gould 11590* (TAES). **San Luis Potosi**: Sta. Catarina, *Rzedowski 6703* (ENCB). **Sinaloa**: Topolobampo, *Palmer 242* (NY). **Sonora**: Morelos, *Santos 1901* (MO); 11 mi S of Norina, *Wiggins & Rollins* in 1941 (MO); 1 mi W of El Tigre, *Santos 1912* (MICH, NY).

UNITED STATES. **Arizona: Cochise Co.**: Texas Canyon, *Deaver 6537* (TAES); Bowier, *Jones 4301* (US); 1 mi S of Portal, *Cazier 965* (NY); Benson, *Griffiths 2002* (US); Ft. Huachuca, *Wilcox* in 1894 (US). **Gila Co.**: White River, *Gould & Robinson 4923* (TAES). **Graham Co.**: Coronado Natl. Forest, *Reeder & Reeder 5526* (ENCB). **Pima Co.**: Tucson, *Pringle 13945* (MO, NY, US); Campus of University, Tuscon, *Hitchcock 3483* (US); Tucson, *Griffiths 3347* (US); Altar to Sasabe, *Griffiths 6916* (US); Sabino Canyon, *Gould 3293* (TAES). **Santa Cruz Co.**: Nogales, *Jones* in 1926 (MO); Patagonia, *Hitchcock 3669* (US). **Arkansas: Conway Co.**: Morrillton, *Larson s.n.* (UARK). **California: Imperial Co.**: Bard, *Goodding & Reeder 1575* (NY, US). **Kern Co.**: 7.2 mi E of Delano, *Twisselmann 8965* (TAES). **Fresno Co.**: Kerman, *Crampton 7564* (TAES). **San Bernardino Co.**: Highland, *Roos 4945* (NY). **Riverside Co.**: 2 mi N of Indio, *Nobs & Smith 495* (TAES). **Tulare Co.**: 4.5 mi ENE of Pixley, *Howell & True 43985* (TAES). **Georgia: Clarke Co.**: 2 mi SE of Athens, *Duncan 29092* (FLAS, NLU). **Lee Co.**: weed in fields, *Andrews s.n.* (FLAS, MISS). **Oconee Co.**: *Brannen n.s.* (FLAS). **Illinois: Union Co.**: 3 mi SW of Wolf Lake, *Evers 107321* (MO). **Kentucky: Fulton Co.**: Hickman, *Athey 1971* (VDB). **Louisiana: Avoyelles Parish**: Effie, *Allen 8745* (NLU). **Caddo Parish**: 15 mi SE of Shreveport, *MacRoberts 1829* (TAES); E of Cottonport, *Schefler & Yoder s.n.* (LSU). **Madison Parish**: Delta, *Thomas 54480* (NLU). **Morehouse Parish**: 6 mi S of Mer Rouge, *Thomas 460* (NLU). **Red River Parish**: SW of Coushatta, *Lasseigne 944* (SMU). **Mississippi: Coahoma Co.**: 1.5 mi E of Lula, *McDaniel 1211* (MO); SE of Lula, *McDaniel 7100* (FLAS, VDB). **Bolivar Co.**: N of Cleveland, *Jacob 530* (US). **Forrest Co.**: Hattiesburg, *Rogers 8500* (VDB). **Issaquenna Co.**: Albemarla Lake, *Rogers 8709* (TENN). **Lincoln Co.**: Brookhaven, *Rogers & Watson 8491-F* (NY). **Oktibbeha Co.**: State College, *Ray 8704* (USF). **Sharkley Co.**: 7 mi SE of Rolling Fork, *Ray 4886* (NY). **Washington Co.**: Delta Center, *Gunn 10816* (MISS). **New Mexico: Dona Ana Co.**: Mesilla Valley, *Standley 477* (MO); Las Cruces, *Hitchcock* in 1904 (US). **Oklahoma: Payne Co.**: Stillwater, *Kiltz 195* (US). **Tennessee: Knox Co.**: Knoxville, *Deselm s.n.* (TENN). **Lake Co.**: Mississippi River at end of Hwy 21, *Rogers 42832* (TENN); Reel Foot Lake, *Rogers 33672* (TENN). **Texas: Brewster Co.**: Alpine, *Warnock T224* (US). **Culberson Co.**: 9K Ranch, *Burgess 545* (TAES). **El Paso Co.**: El Paso, *Hitchcock 13326* (US). **Presidio Co.**: Marfa, *Silveus 2377* (TAES); Marfa, *Hinckley 1226* (NY).

Fig. 1. *Eriochloa acuminata* (Presl) Kunth var. *acuminata* (*Shaw 2091*): A. Habit (× 1/2); B. Portion of inflorescence branch (× 5); C. Spikelet (× 12); D. Upper floret (× 12); E. Ligule (× 2).

ERIOCHLOA ACUMINATA var. **minor** (Vasey) R.B. Shaw, comb. nov. *Eriochloa punctata* (L.) Desv. ex Hamilt. var. *minor* Vasey, Contr. U.S. Natl. Herb. 3:21. 1892. TYPE: UNITED STATES. TEXAS, *Wright 2087, Neally.* This herbarium sheet consists of two plants. The specimen on the right is the type, while the plant on the left is a specimen of *E. lemmonii*. It is impossible to tell whether the type specimen was collected by Wright or Neally (LECTOTYPE: US!). *Eriochloa gracilis* (Fourn.) Hitchc. var. *minor* (Vasey) Hitchc., J. Wash. Acad. Sci. 23:456. 1933.

Habitat and distribution: Infrequent as a weed along roadsides, irrigated fields, orchards and other disturbed areas in the southwestern U.S., central and northern Mexico, also adventive in Maryland.

Representative specimens: MEXICO. **Chihuahua**: La Campa, *Valdes VR-114* (NY). **Coahuila**: 5 mi S of Castanos, *Reeder, Reeder & Soderstrom 3282* (US). **Durango**: 4 mi E of La Zarca, *Reeder, Reeder & Godding 1669* (ENCB). **Jalisco**: 7 – 8 mi S of Acatlan de Juarez, *McVaugh 19454* (US); 7 km al S de Acatlan, *Rzedowski 29345* (ENCB). **Mexico**: Vallanda, *Hinton 6367* (ENCB, NY). **Michoacan**: Morelia, *Arsene 5106* (MO), *33600* (US). **Queretaro**: *Rzedowski 16354* (ENCB). **Sonora**: Colonia Morelos, *Santos 2024* (ENCB); NE of El Tigre, *Santos 1943* (NY, US); 25 mi W of La Angostura, *Santos 1835* (NY).

UNITED STATES. **Arizona**: **Cochise Co.**: Chiricahua Mts., *Gould & Haskell 4619* (NY); Tombstone, *Reeder & Reeder 6276* (ENCB); Douglas, *Jones* in 1932 (US). **Pima Co.**: north slope of Santa Rita Mts., *Griffiths 7008* (US); Santa Rita Mts., *Gould 4479* (TAES), *Silveus 3492* (TAES); 40 mi from Tucson, *Gould & Haskell 3273* (US). **Santa Cruz Co.**: 4 mi SW of Patagonia, *Pinkava, Lehot, Brown & McLeod 786* (ENCB); Pena Blanco Mts., *Goodding* in 1935 (TAES). **Maryland**: **Baltimore Co.**: Canton, *Reed 32728* (US). **New Mexico**: **Dona Ana Co.**: Pena Blanca, Organ Mts., **Standley** in 1906 (US); Las Cruces, *Spellenberg 4415* (NY); Las Cruces, **Vasey** in 1881 (US); Mesilla Park, *Hitchcock 3822* (US). **Grant Co.**: 15 mi WNW of Silver City, *Barkley 14610* (MO). **Hidalgo Co.**: near Dog Springs, *Spellenberg & Spellenberg 3828* (NY); 19 mi N of Rodeo, *Gould 12035* (TAES). **Luna Co.**: Deming, *Hitchcock 3764* (US). **Texas**: no locality, *Neally* in 1889 (US). **Brewster Co.**: W of Alpine, *Hitchcock 13600* (US). **El Paso Co.**: El Paso, *Hitchcock 13332* (US), *Silveus 5494* (TAES); Hueco tanks, *Waterfall 6611* (MO, NY). **Presidio Co.**: Marfa, *Hinckley 1386* (NY).

ERIOCHLOA ARISTATA Vasey, Bull. Torrey Bot. Club 13:229. 1886. TYPE: MEXICO. CHIHUAHUA: southwestern Chihuahua, *Palmer 110E* (LECTOTYPE: K!).

Plants annual. Cataphylls absent. Flowering culms 4 – 10 dm tall; erect, or decumbent; rooting or not rooting at the lower nodes; 3 – 10-noded. Nodes hairy. Internodes glabrous. Sheaths not overlapping; not inflated; chartaceous; 40 – 130 mm long; smooth; glabrous. Ligule a fringe of hairs (with a minute membranous part); 0.5 – 0.8 mm long (– 2.0). Leaf blades linear to lanceolate; flat; straight to flexuous; spreading; 6 – 20 cm long; 6 – 20 mm wide; adaxially smooth; glabrous on the adaxial surface (rarely pubescent). Prophyllum 40 – 70 mm long. Peduncle 150 – 300 mm long; hairy. Inflorescence 10 – 30 mm wide. Main axis 50 – 200 mm long; hairy. Primary branches appressed to the main axis to spreading; 16 – 30 on the main axis; 20 – 35 mm long; 0.3 – 0.5 mm

wide; not winged; hairy; setose; with loosely, or neatly arranged spikelets. Pedicels 0.5 − 2 mm long; hairy; with glabrous apices. Spikelets 20 − 35 on a typical primary branch; paired; not divergent from the axis; lanceolate; 4 − 8 mm long; 1.1 − 1.6 mm wide. First glume absent. Second glume 1 − 1.1 × the length of the lower floret; lanceolate; 5-nerved; hairy; acuminate; awned. Second glume awn 1.5 − 3.5 mm long. Sterile floret lacking stamens. Lemma of the sterile floret lanceolate; 4 − 8 mm long; 1.1 − 1.6 mm wide; 3 − 7-nerved; the surface hairy; setose; acuminate; muticous to mucronate (the mucro less than 0.4 mm long). Palea of sterile floret absent. Fertile floret 0.45 − 0.6 × the length of the sterile floret. Lemma of fertile floret elliptic, 3 − 4 mm long (2 − 6); 5-nerved; acute to rounded; mucronate or awned. Lemma of fertile floret awn 0.2 − 0.8 mm long. Chromosome number $2n = 36$ for the typical variety (Gould & Soderstrom 1967) and var. *boxiana* (*Gould 12677*).

KEY TO THE VARIETIES OF ARISTATA

Spikelets more than 6.4 mm long, if shorter, then the mucro of the upper floret not over 0.3 mm long; panicle spreading or loosely contracted; plants usually not rooting at the lower nodes ..... var. *aristata*

Spikelets usually less than 6.5 mm long; awn of the upper floret usually over 0.3 mm long; panicles tightly contracted; plants usually rooting at the lower nodes ..... var. *boxiana*

ERIOCHLOA ARISTATA var. ARISTATA. Fig. 2.

Eriochloa punctata (L.) Desv. ex Hamilt. var. *aristata* (Vasey) Jones, Contr. West. Bot. 14:11. 1912.

Habitat and distribution: Weed in moist swales, roadsides and irrigated fields from the southwestern U.S. throughout northern and central Mexico.

Representative specimens: MEXICO. **Chihuahua: Rio Bonito,** *LeSuer MEX-094* (MO); 5 mi N of Parral, *Reeder, Reeder & Goodding 1686* (ENCB). **Durango**: about 45 mi S of Parral, *Reeder, Reeder & Goodding 1677* (ENCB). **Guerrero**: 1 mi N of Grutas, *Gould 9589* (TAES); 12 km al N de Buenavista, *Rzedowski 26913* (ENCB). **Jalisco**: 8 km al N de Cruz de Loreto, *Rzedowski 1322* (MICH). **Morelos**: 20 km NE Cuoatla, *Boyd 47* (MICH); km 126, Cuernavaca-Taxco Hwy, *Lundell & Lundell 12567* (MICH). **Nayarit**: 10 km E of the village of Jesus Maria, *Feddema 1385* (MICH). **Sinaloa**: Culican, *Palmer 1548* (MICH, NY, US); 7 mi NE of El Quintero, *Breedlove & Thorne 18095* (TAES); Valle de Carrizo, Rodriguez 1603 (ENCB); 55 mi NW of Mazatlan, *Waterfall 12769* (MICH, US). **Sonora**: Alamosa, *Palmer* in 1890 (F, NY); 19 mi N of Obregon, *Gould 12085* (TAES); 1 mi NE of El Zapo, *Wiggins & Rollins 276* (MICH, MO, NY); Colonia Morelos, *Santos 2024* (MO); 35 km al NW de Altar, *Araiza 106* (MICH); 37 mi N of Hermosillo, *Waterfall 12879* (MICH).

UNITED STATES. **Arizona**: **Pima Co.**: Campus University of Arizona, Tucson, *Griffiths 1612* (NY, US); near San Miguel, *Weatherwax 2777* (TAES); Tucson, *Thornber 98*

(NY, MO, US); Coyote Mountains, *Reeder, Reeder & Goodding* in 1943 (US); Sabino Canyon, Santa Catalina Mountains, *Gould 3292* (TAES). **California**: **Imperial Co.**: Bard, U.S. Yuma Field Station, *Reeder 2572* (NY, MO, TAES); Colorado River, Ft. Yuma, *Parish 8232* (US). **Mississippi**: **Oktibbeha Co.**: State College, *McDaniel 2207* (MO).

Fig. 2. *Eriochloa aristata* Vasey var. *aristata* (*Gould 3292*): A. Habit (× 1/2); B. Portion of inflorescence branch (× 4); C., Spikelet (× 9); D. Upper floret (× 9); E. Ligule (× 3).

ERIOCHLOA ARISTATA var. **boxiana** (Hitchc.) R.B. Shaw, stat. et comb. nov. *Eriochloa boxiana* Hitchc., Publ. Carnegie Inst. Wash. Publ. 436:339, 1934. TYPE: ANTIGUA. near Parry's Bridge, in damp, almost swampy, open abandoned land, frequent; but extremely local, 7 Sep 1931, *Box 43* (HOLOTYPE: US!; ISOTYPE: K!).

Habitat and distribution: Swamps, coastal lowlands and marshes, mud flats along ponds from Mexico to Guatemala, El Salvador and Colombia. Only report from the Caribbean is the type collection from Antigua.

Representative specimens: **EL SALVADOR. Sonsonate**: Acajutla, *Rohweder 1639* (MO). **GUATEMALA. Jutiapa**: between railroad station of Mita and town of Asuncoin Mita, *Steyermark 31779* (F, US). **Zacapa**: near Estanzuela, *Steyermark 29056* (F, US). **MEXICO. Chiapas**: E shore of Mar Muerto, N of Paradon, *Breedlove & Thorne 20788* (MICH); at outskirts of Paradon, *Gould 12677* (TAES, US). **Nayarit**: Matachen, *McVaugh 19451* (US). **Oaxaca**: 4 km N of Estacion Don, *Breedlove & Thorne 18635* (TAES); 4 km NNE of Tehauntepec, *King 1363* (US). **Vera Cruz**: 10 mi NW of Vera Cruz, *Harvey 85599* (MICH). **Yucatan**: Progreso, *Swallen 2496* (US), *2932* (US), *2959* (US); Progreso to Merida, *Swallen 2377* (US).

ERIOCHLOA CONTRACTA Hitchc., Proc. Biol. Soc. Wash. 41:163. 1928.

Fig. 3. *Helopus mollis* C. Muell., Bot. Zeitung (Berlin) 19:314. 1861, non *Eriochloa mollis* Kunth 1829. TYPE: UNITED STATES. TEXAS: Gonzales, *Drummond 370* (HOLOTYPE: K!; fragment US!).

Plants annual. Cataphylls absent. Flowering culms 2 – 10 dm tall; erect, or decumbent; rooting or not rooting at the lower nodes; 2 – 5-noded. Nodes hairy. Internodes glabrous, or hairy; pubescent. Sheaths not overlapping; not inflated; chartaceous; 40 – 80 mm long; smooth; glabrous or hairy; pubescent. Ligule a fringe of hairs (with a minute membranous part at the base); 0.4 – 1.1 mm long. Leaf blades linear; flat to conduplicate; straight; appressed to the culm to spreading; 8 – 12 cm long (6 – 22); 2 – 8 mm wide; adaxially smooth; hairy on the adaxial surface. Prophyllum 25 – 45 mm long. Peduncle 90 – 240 mm long, hairy. Inflorescence 3 – 12 mm wide. Main axis 60 – 200 mm long, hairy. Primary branches appressed to the main axis; 10 – 20 on the main axis (– 28); 15 – 45 mm long (– 60); 0.25 – 0.35 mm wide; not winged; hairy; pubescent to setose; with neatly arranged spikelets. Pedicels 0.2 – 1 mm long; hairy; with glabrous apices. Spikelets 8 – 16 on a typical primary branch; solitary (occasionally paired at the base); not divergent from the axis; lanceolate; 3.5 – 4.5 mm long (3.1 – 5.5); 1.2 – 1.7 mm wide. First glume absent. Second glume 1 × the length of the lower floret; lanceolate; 3 – 9-nerved; hairy; acuminate; awned. Second glume awn 0.4 – 1 mm long. Sterile floret lacking stamens. Lemma of the sterile floret lanceolate; 3 – 4.3 mm long; 1.2 – 1.7 mm wide; 3 – 7-nerved; the surface hairy; setose; acumi-

nate; muticous, or mucronate. Palea of sterile floret absent. Fertile floret 0.65 – 0.72 × the length of the sterile floret. Lemma of fertile floret elliptic; 2 – 2.5 mm long; acute to rounded; awned. Lemma of fertile floret awn 0.4 – 1.1 mm long. Chromosome number $2n = 36$ (Brown 1950; Gould 1968; *Shaw 2000* and *2001*).

Eriochloa contracta appears closely related to *E. acuminata* and intermediate forms may be expected in the southwestern U.S. *Eriochloa contracta* is easily distinguished from *E. acuminata* by the long awn of the upper lemma and tightly contracted and almost cylindrical panicle. Occasionally, *E. contracta* may be confused with the perennial *E. punctata* that is flowering the first year; however, *E. punctata* has glabrous leaves, narrower and more tapering spikelets and longer awn on the upper lemma.

Habitat and distribution: Growing as a weed in fields, ditches and other disturbed areas. Widespread in Texas, Oklahoma, Kansas and extending into Nebraska and Missouri. Adventive eastward in Alabama, Louisiana, Mississippi, Indiana, Illinois, Virginia and westward into New Mexico, Colorado and California. Reported from northern Mexico (Gould 1975), but no Mexican collections were examined by the authors.

Representative specimens: UNITED STATES. **Alabama**: east central Alabama, *Wilson* in 1947 (US). **Arkansas**: **Arkansas Co.**: near St. Charles, *Oliver s.n.* (UARK). **Miller Co.**: Texarkana, *Hopkins s.n.* (UARK). **Phillips Co.**: Helena, *Hodson s.n.* (UARK). **Poinsett Co.**: Lepanto, *Moore 55-444* (UARK). **Washington Co.**: near White River, *Guess 52* (UARK). **California**: **Imperial Co.**: 5 mi W of El Centro, *Nobs & Smith 562* (TAES). **Solano Co.**: 4.8 mi N of Dixon, *Crampton 3148* (US). **Colorado**: **Bent Co.**: W of Wiley, *Lane* in 1942 (US). **Indiana**: **Harrison Co.**: 0.2 mi W of jct of 460-462, *Terrell & Meyer 4319* (WYO). **Illinois**: **Union Co.**: near Aldridge, *Van Schaak 3514* (MO). **Kansas**: **Barton Co.**: 9 mi E of Hoisington, *Hydberg & Imler 1292* (MO). **Butler Co.**: near Potwin, *Chase 3333* (US). **Clark Co.**: *Carleton 520* (US). **Coffey Co.**: 6 mi E of Le Roy, *Ungar 1028* (US). **Douglas Co.**: Lawrence, *Horr & McGregor 4082* (US). **Shawnee Co.**: 1 mi S of Big Springs, *Ireland 154* (US). **Sumner Co.**: Caldwell, *Smyth 266* (US). **Waubaunsee Co.**: US 40 and K 99, *Robinson 1018* (US). **Woodson Co.**: 1 mi W of Yates Center, *Lathrop 1580* (US). **Louisiana**: **Caddo Parish**: 14 mi SSE of Shreveport, *MacRoberts 1481* (TAES). **Madison Parish**: NE of Waverly, *Thomas et al. 6555* (NLU). **Natchitoches Parish**: 2.5 mi SE of Natchez, *Thieret 31782* (DUKE). **Quacita Parish**: N of Monroe, *Thomas 30404* (NLU). **Red River Parish**: 1.3 mi SE of Grand Bayou, *Shinners 24755* (SMU). **Richland Parish**: 3 mi N of Bee Bayou, *Thieret 23821* (US, DUKE). **Tensas Parish**: Saranac, *Briley 1776* (NLU). **Winn Parish**: SW corner, *Kessler 1699* (NLU). **Mississippi**: **Bolivar Co.**: Duncan, *Pullen 70428* (MISS). **Coahoma Co.**: 4 mi W of Clarksdale, *Pullen 70449* (MISS). **DeSota Co.**: Horn Lake, *Rogers 46082* (VDB). **Quitman Co.**: 5 mi NW of Darling, *Pullen 70799* (MISS). **Sunflower Co.**: Doddsville, *Jacob 784* (US); SW of Sunflower, *Pullen 67919* (MISS). **Washington Co.**: Greenville, *Shinners 32370* (SMU). **Missouri**: **Jackson Co.**: Sheffield, *Bush 769* (MO); Independence, *Castaner 4399* (MO). **Pemiscot Co.**: 4 mi E of Hayward, *Steyermark 79449* (US). **Pike Co.**: SE of Ashburn, *Steyermark 66654* (US). **St. Louis Co.**: N of St. Louis, *Muehlenbach 3654* (MO); W of St. Louis, *Pohl 12989* (MO). **Nebraska**: **Lancaster Co.**: near Lincoln, *Robertson* in 1938 (US). **Douglas Co.**: University

Fig. 3. *Eriochloa contracta* Hitchc. (*Shaw 2195*): A. Habit (× 1/2); B. Portion of inflorescence branch (× 5); C. Spikelet (× 10); D. Upper floret (× 10); E. Ligule (× 4).

of Nebraska at Omaha Campus, *Sutherland 2752* (NY). **New Mexico. Chavez Co.**: S of Roswell, *Hinckley & Hinckley 253* (US). **Dona Ana Co.**: Mesilla Valley, *Wooton & Standley 3263* (NY). **Eddy Co.**: Carlsbad, *Hitchcock 13475* (US). **Oklahoma: Alfalfa Co.**: S of Burlington, *Pederson 21* (TAES). **Carter Co.**: 2 mi W of Ardmore, *Waterfall 5580* (NY). **Cleveland Co.**: 3 mi N of Norman, *Nighswonger 419* (TAES). **Comanche Co.**: Wichita Mountains Wildlife Refuge, *McMurry 993* (US). **Jackson Co.**: Altus, *Stevens 1179* (US). Kay Co.: no locality, *White* in 1898 (NY). **Payne Co.**: Stillwater, *Hitchcock 15178* (US). **Texas Co.**: 8 mi SW of Guymon, *Williams 128* (TAES). **Woods Co.**: NW of Alva, *Nighswonger 1232* (TAES). **Texas: Baylor Co.**: 6.3 mi ENE of Mabelle, *Shinners 20771* (TAES). **Bell Co.**: 1 mi N of Sparks, *Wolff 2700* (TAES). **Brazos Co.**: A&M Campus, *Gould 6141* (TAES). **Brisco Co.**: 23 mi E of Silverton, *Gould & Thomas 7715* (TAES). **Brown Co.**: Brownwood, *Deberry 8* (TAES). **Calhoun Co.**: 7 mi N of Port La Vaca, *Munoz 1219* (US). **Callahan Co.**: 9 mi S of Baird, *Cory 58382* (TAES). **Dallas Co.**: Dallas, *Reverchon 13114* (MO). Denton Co.: *Gould 10295* (TAES). **El Paso Co.**: El Paso, *Hitchcock 13325* (US). **Galveston Co.**: Galveston Island, *Tharp 43084* (NY). **Hale Co.**: 7 mi S of Plainview, *Gould 7155* (TAES). **Hardeman Co.**: Chillicothe, *Ball 980* (US). **Hemphill Co.**: near Canadian, *Eggert* in 1900 (MO). **Howard Co.**: Big Spring, *Hitchcock 13420* (US). **Jack Co.**: 2 mi NE of Jacksboro, *Gould 10285* (TAES). **Jackson Co.**: Lavaca River, *Tharp* in 1941 (MO). **Karnes Co.**: 0.6 mi NW of Kenedy, *Johnson 1060* (TAES). **Kerr Co.**: Kerr Wildlife Management Area, *Gould 8300* (TAES). **Kleberg Co.**: Kingsville, *Piper* in 1906 (US). **McLennan Co.**: near Moore & Pitts, *Smith 795* (US). **Montgomery Co.**: Magnolia, *Thurow* in 1915 (US). **Navarro Co.**: 13 mi S of Corsicana, *Reed 34967* (TAES). **Nolan Co.**: Roscoe, *Johnson, York & Tharp 43103* (MO). **Nueces Co.**: Corpus Christi, *Hitchcock 5377* (US). Oldham Co.: Vega, *Gould 14337* (TAES). **Rockwall Co.**: no locality, *Nees* in 1923 (TAES). **San Patricio Co.**: Welder Wildlife Foundation, *Lagford 83* (TAES). **Sutton Co.**: Texas Agricultural Experiment Station, *Cory 34976* (TAES). **Tarrant Co.**: 1 mi N of Saginaw, *Whitehouse 16267* (NY). **Throckmorton Co.**: NE of Throckmorton, *Parks & Cory 15872* (TAES). **Webb Co.**: Laredo, *Hitchcock 5513* (US). **Wichita Co.**: Burkburnett, *Tharp 134* (US). **Virginia: Arlington Co.**: near Glencarlyn, *Blake 11675A* (US).

ERIOCHLOA DISTACHYA Kunth, Nov. Gen. et Sp. 1:95, pl. 30. 1816. Fig. 4. TYPE: VENEZUELA. Crescit in ripa Orincoci fluminis inter Santa Barbara et Esmeralds (HOLOTYPE: fragment US!).

Helopus brachystachya Trin., Sp. Gram. Icon. t. 277. 1831. *Paspalum brachystachyum* (Trin.) Trin., Mem. Acad. Imp. Sci. St. Petersbourg, Ser. 6, Sci. Nat. 1:133. 1834.

Plants perennial; lacking rhizomes. Cataphylls absent. Flowering culms 1 – 5 dm tall; erect, or decumbent; rooting or not rooting at the lower nodes; 2 – 5-noded. Nodes hairy. Internodes glabrous (frequently pubescent at the apex). Sheaths overlapping or not overlapping; not inflated; chartaceous; 20 – 40 mm long; smooth; glabrous, or hairy; pubescent to pilose. Ligule a fringe of hairs; 0.2 – 1.2 mm long. Leaf blades filiform to linear; flat; straight; appressed to the culm to spreading; 6 – 14 cm long; 1.5 – 5 mm wide; adaxially smooth; hairy on the adaxial surface (occasionally nearly glabrous). Prophyllum 20 – 40 mm long. Peduncle 100 – 250 mm long; hairy. Inflorescence 3 – 30 mm wide. Main axis 0 – 25 mm long; hairy. Primary branches speading; 1 – 3 on the main

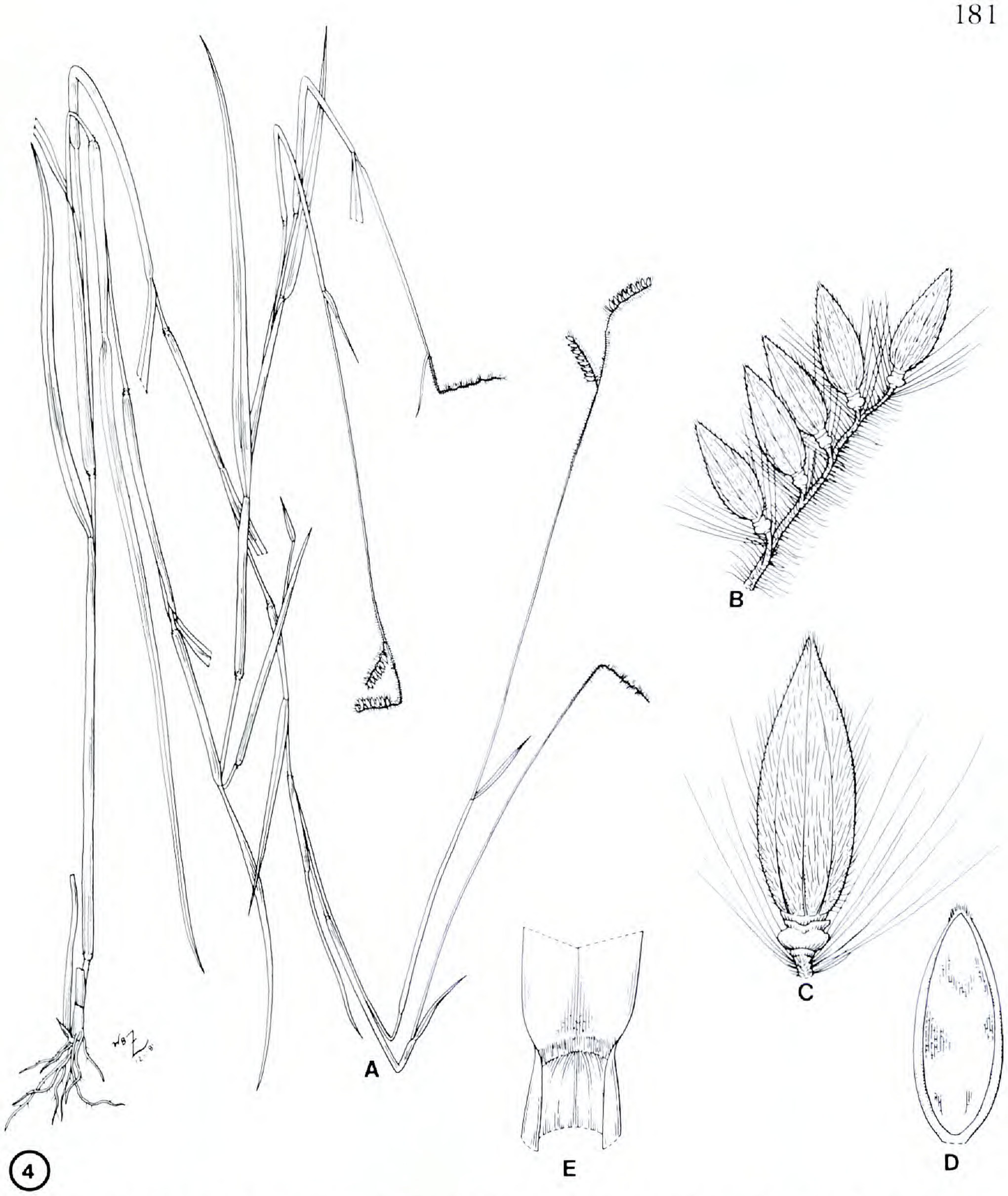

Fig. 4. *Eriochloa distachya* Kunth (*Anderson 9773*): A. Habit (× 1/2); B. Portion of inflorescence branch (× 5); C. Spikelet (× 12); D. Upper floret (× 12); E. Ligule (× 6).

axis (−4); 10−20 mm long; 0.4−0.7 mm wide; not winged; hairy; pilose; with neatly arranged spikelets. Pedicels 0.4−0.7 mm long; hairy (the hairs 4−5 mm long) with hairy apices. Spikelets 12−30 on a typical primary branch; solitary; divergent from the axis; lanceolate to ovate; 3.2−4.4 mm long; 1.1−1.3 mm wide. First glume absent. Second glume 1 × the length of the lower floret; lanceolate to ovate; 5− or 7-nerved; hairy; acuminate to acute; muticous. Sterile floret lacking stamens (rarely staminate). Lemma of the sterile floret lanceolate to ovate; 2.5−3.7 mm

long; 1.1 – 1.3 mm wide; 5-nerved; the surface hairy; setose; acute; muticous. Palea of sterile floret fully developed or absent; hyaline. Fertile floret 0.8 – 0.9 × the length of the sterile floret. Lemma of fertile floret ovate; 2.2 – 2.5 mm long; acute to rounded; muticous (or minutely mucronate). Chromosome number $2n = 18$ (Pohl & Davidse 1971).

Habitat and distribution: In wet savannas and grasslands at elevations from 0 – 600 meters. Infrequent in Central America (Costa Rica, Guatemala, Panama) becoming more common in South America (Bolivia, Peru, Brazil, Colombia, Paraguay and Venezuela).

Representative specimens: COSTA RICA. **Puntarenas**: 3 km N of Carretera Interamericana, *Pohl & Davidse 1159* (F). **Osa**: no locality, *Tonduz 4622* (US). GUATEMALA. **Alta Verapaz**: hills between Cajal and Cahabon, *Pittier 220* (US). PANAMA. **Cocle**: vicinity of Ola, *Pittier 5043* (NY, US). **District of Panama**: in savanna, Rio Tocumen, *Standley 29298* (US); wet savanna near the big swamp E of Rio Tocumen, *Standley 26613* (MO, US); Tatana River, *Killip 4228* (NY, US); between Las Sabanas and Matias Hernandez, *Standley 31861* (US).

ERIOCHLOA FATMENSIS (Hochst. & Steud.) W.D. Clayton, Kew Bull. 30:108. 1975. Fig. 5. *Panicum fatmense* Hochst. & Steud. *in. sched.*, Schimper It. Un.:806. 1837. TYPE: SAUDI ARABIA. MECCA: *Schimper 806* (ISOTYPE: K!). *Helopus acrotrichus* Steud., Syn. Pl. Glum. 1:100. 1854, *nom. superfl.* Based on *Panicum fatmense* Hochst. & Steud.

Helopus nubicus Steud., Syn. Pl. Glum. 1:100. 1854. *Eriochloa nubica* (Steud.) Thell. in Viert. Nat. Ges. Zurich 64:697. 1919.

Plants annual. Cataphylls absent. Flowering culms 3 – 12 dm tall; erect, or decumbent; rooting or not rooting at the lower nodes; 2 – 5-noded. Nodes glabrous. Internodes glabrous. Sheaths not overlapping; not inflated; chartaceous; 30 – 70 mm long; smooth; glabrous. Ligule a fringe of hairs; 0.5 – 1 mm long. Leaf blades linear; flat to involute; straight; spreading; 6 – 40 cm long; 3 – 8 mm wide; adaxially smooth; glabrous on the adaxial surface. Prophyllum 25 – 100 mm long. Peduncle 100 – 200 mm long; glabrous. Inflorescence 8 – 30 mm wide. Main axis 60 – 180 mm long; smooth, or scabrous. Primary branches appressed to the main axis to spreading; 3 – 10 on the main axis; 25 – 60 mm long; 0.4 – 0.6 mm wide; winged to not winged; glabrous; with loosely arranged spikelets. Pedicels 0.2 – 0.8 mm long; glabrous or hairy; with glabrous apices (frequently with a few short hairs about 0.5 mm long). Spikelets 20 – 40 on a typical primary branch; solitary, or paired; not divergent from the axis; lanceolate; 2.7 – 3.3 mm long; 0.8 – 1 mm wide. First glume absent. Second glume 1.1 – 1.3 × the length of the lower floret; lanceolate; 5-nerved; hairy; acuminate; mucronate to awned. Second glume awn 0.3 – 1.5 mm long. Sterile floret lacking stamens. Lemma of the sterile

Fig. 5. *Eriochloa fatmensis* (Hochst. & Steud.) W.D. Clayton (*Beetle RR-122*): A. Habit (× 1/2); B. Portion of inflorescence branch (× 6); C. Spikelet (× 12); D. Upper floret (× 12); E. Ligule (× 5).

floret lanceolate; 2.5 – 3.4 mm long; 0.8 – 1 mm wide; 5-nerved; the surface hairy; setose; acuminate; mucronate. Palea of sterile floret absent. Fertile floret 0.65 – 0.75 × the length of the sterile floret. Lemma of fertile floret elliptic; 1.7 – 2.2 mm long; acute to rounded; awned. Lemma of fertile floret awn 0.25 – 0.5 mm long. Chromosome number unknown.

Previous authors (Nash 1912; Gould 1950) used the name *Eriochloa procera* (Retz.) C.E. Hubb. for these specimens. *Eriochloa procera*, a native of tropical Asia and Australia, is distinguished from *E. fatmensis* primarily on spikelet shape. Spikelets of *E. procera* are acute at the apex, whereas those of *E. fatmensis* are acuminate with the second glume frequently awned. Otherwise, the species are identical. The relationship between *E. fatmensis* and the Australian species, *E. decumbens* Bailey, is unclear.

Habitat and distribution: Growing in wet areas, ditches and grasslands throughout the tropics of Africa and extending into Arabia and India. Introduced in the New World. Rare and probably not a permanent component of the flora.

Representative specimens: UNITED STATES. **Arizona: Pima Co.**: University of Arizona Campus, Tucson, *Griffiths 1516* (US). **Mississippi: Harrison Co.**: Biloxi, *Tracy 6112* (TAES).

ERIOCHLOA LEMMONII Vasey & Scribner, Bot. Gaz. (Crawfordsville) 9:185, pl. 2. 1884. Fig. 6. TYPE: UNITED STATES. ARIZONA: Huachuca Mts., Jun 1882, *Lemmon 2910* (LECTOTYPE: US!).

Plants annual. Cataphylls absent. Flowering culms 2 – 8 dm tall; erect or decumbent; rooting or not rooting at the lower nodes; 2 – 5-noded. Nodes hairy. Internodes hairy; pubescent to pilose. Sheaths not overlapping; conspicuously inflated, or not inflated; chartaceous; 40 – 90 mm long; smooth; hairy; pubescent to pilose. Ligule a ciliate membrane to a fringe of hairs; 0.5 – 1 mm long. Leaf blades lanceolate; flat; straight; spreading; 5 – 15 cm long; 6 – 20 mm wide; adaxially smooth; hairy on the adaxial surface. Prophyllum 15 – 30 mm long. Peduncle 120 – 180 mm long; hairy. Inflorescence 5 – 40 mm wide. Main axis 50 – 150 mm long; hairy. Primary branches appressed to the main axis to spreading; 3 – 8 on the main axis (2 – 10); 10 – 40 mm long; 0.4 – 0.6 mm wide; not winged; hairy; setose; with loosely arranged spikelets. Pedicels 0.5 – 1 mm long; hairy; with hairy or glabrous apices. Spikelets 10 – 24 on a typical primary branch; paired (becoming solitary towards the apex); not divergent from the axis; elliptic; 3.5 – 4.5 mm long (3 – 4.9); 1.2 – 1.7 mm wide. First glume absent. Second glume 1 × the length of the lower floret; elliptic; 5 – 7-nerved; hairy (to nearly glabrous); acute; muticous. Sterile floret staminate, or lacking stamens. Lemma of the sterile floret

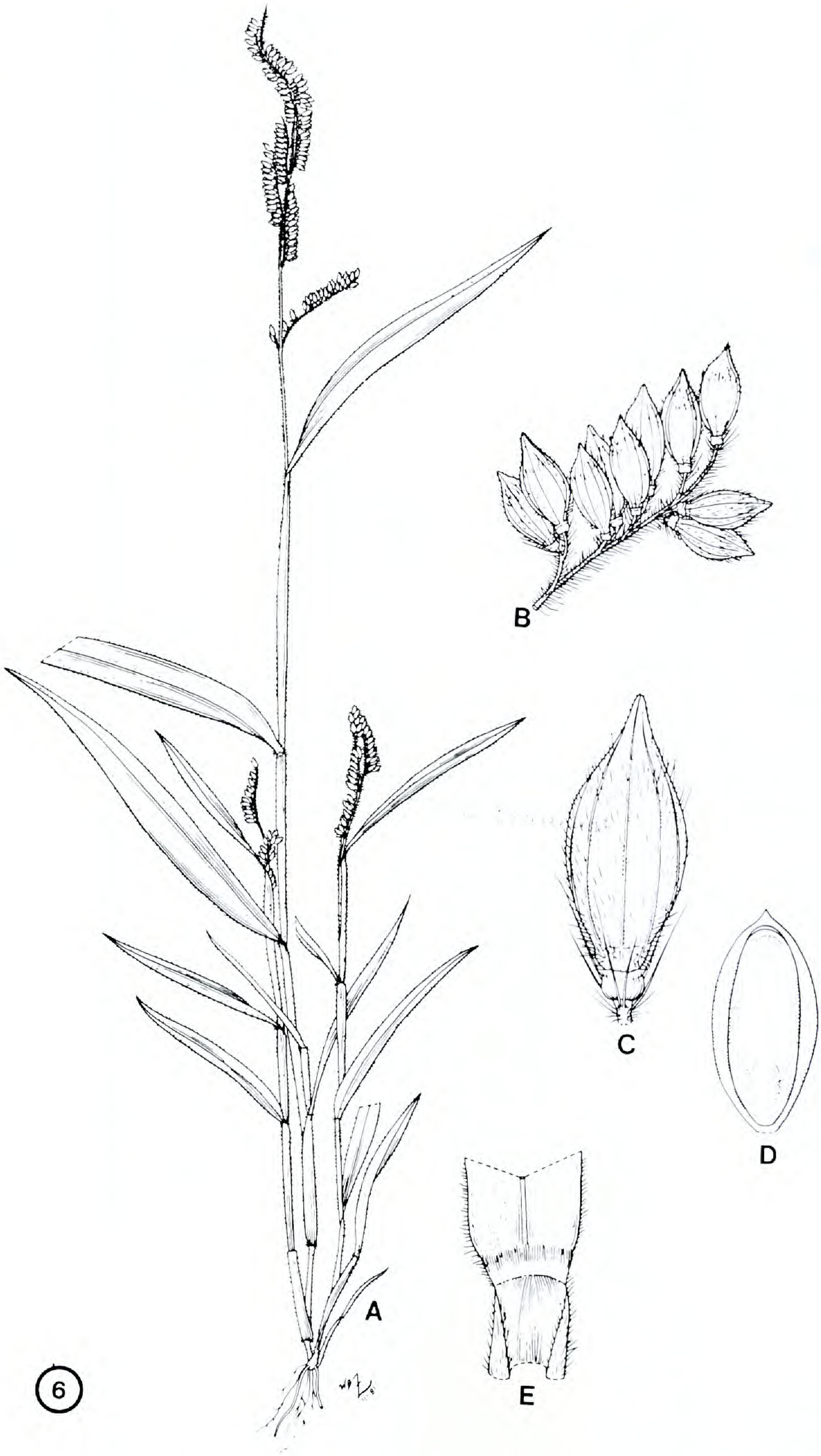

Fig. 6. *Eriochloa lemmonii* Vasey & Scribner (*Pena & Gonzales 723*): A. Habit (× 1/2); B. Portion of inflorescence branch (× 5); C. Spikelet (× 12); D. Upper floret (× 12); E. Ligule (× 6).

elliptic; 2.7 − 4 mm long; 1.2 − 1.7 mm wide; 5-nerved; the surface hairy; setose to pilose; acute; muticous. Palea of sterile floret fully developed, or vestigial; hyaline. Fertile floret 0.85 − 0.95 × the length of the sterile floret. Lemma of fertile floret elliptic; 2.3 − 3.3 mm long; acute to rounded; muticous, or mucronate. Chromosome number $2n = 36$ (Reeder 1967).

This species apparently hybridizes with *E. acuminata* and intermediate specimens are present in southern Arizona and New Mexico. Gould (1950), because of these intermediate plants, merged the two taxa. *Eriochloa lemmonii* can be distinguished from *E. acuminata* by the frequent presence of a hyaline palea of the lower floret, the distinct raised nerves on the second glume and lower lemma, the broad velvety pubescent leaf blades, the blunt spikelets and the lack of a distinctly mucronate tipped lemma of the upper floret. Possible hybrids between the two taxa lack the lower palea and narrower leaf blades which are sparsely pubescent to puberulent. The intermediates, as well as *E. lemmonii*, usually have long terminal hairs on the pedicels. Plants that also are possible intermediates between *E. lemmonii* and *E. nelsonii* occur in central Mexico, especially in the state of Jalisco. These specimens, referred to as *E. nelsonii* var. *papillosa*, retain the general appearance of *E. nelsonii* but are frequently less pubescent on the rachis, pedicel, and spikelet, the spikelets are shorter than 6 mm and the lemma and palea are rough, due to the presence of compound papillae on the surface.

Habitat and distribution: Rare in canyons and on rocky slopes in southern Arizona, Chihuahua and Sonora, Mexico.

Representative specimens: MEXICO. no locality, *Palmer* in 1884 (TAES). **Chihuahua**: canon de Hepari, N of Aribabi, *Harvey 1652* (MICH, US); Rio Negro, *LeSuer 0174* (US); SW Chihuahua, *Palmer 100a* (NY, US); entre Barrancas del Cobre y Bacahipare, *Pena & Gonzales 728* (ENCB); Mojarachic, *Knoblock 5459* (F). **Sinaloa**: 9 mi SW of Santa Lucia, *Reeder & Reeder 4458* (US). **Sonora**: Horconcitos, Arroyo del Salto, *White 3760* (MICH).

UNITED STATES: **Arizona**: **Pima Co.**: Sycamore Canyon, *Goodding* in 1937 (US); Nogales, *Peebles & Harrison 4703* (US).

ERIOCHLOA MICHAUXII (Poir.) Hitchc., Contr. U.S. Natl. Herb. 12:147. 1908. *Panicum michauxii* Poir. in Lam., Encycl. Sup. 4:278. 1816. TYPE: UNITED STATES. FLORIDA: in sabulosis maritimis Florida, lieux tres humides a 15 mi de St. Augustin, *Michaux* (HOLOTYPE: P).

Plants perennial; rhizomatous (usually not present on herbarium specimens). Cataphylls present. Flowering culms 5 − 25 dm tall; erect; not rooting at the lower nodes; 3 − 7-noded. Nodes hairy. Internodes glabrous. Sheaths not overlapping; not inflated; chartaceous; 60 − 300 mm long; smooth; glabrous. Ligule a fringe of hairs; 0.5 − 1.5 mm long. Collar

Fig. 7. *Eriochloa michauxii* (Poir.) Hitchc. var. *michauxii* (*Curtiss 3600*): A. Habit (× 1/2); B. Portion of inflorescence branch (× 3); C. Spikelet (× 12); D. Upper floret (× 12); E. Ligule (× 1).

hairy. Leaf blades linear; flat to conduplicate; straight to flexuous; spreading; 10 – 60 cm long; 5 – 15 mm wide; adaxially smooth; glabrous on the adaxial surface. Prophyllum 60 – 120 mm long. Peduncle 200 – 400 mm long; hairy. Inflorescence 25 – 100 mm wide. Main axis 100 – 300 mm long; hairy. Primary branches spreading; 10 – 25 on the main axis; 15 – 60 mm long; 0.5 – 0.8 mm wide; not winged; hairy; pilose to setose; with loosely arranged spikelets. Pedicels 0.3 – 2.5 mm long; hairy; with glabrous apices. Spikelets 16 – 40 on a typical primary branch; solitary or paired; not divergent from the axis; ovate (approaching elliptic); 4 – 5.5 mm long (3.7 – 5.7); 1.3 – 1.8 mm wide. First glume absent. Second glume 1 × the length of the lower floret; ovate; 5-nerved; hairy; acute; muticous (rarely mucronate). Sterile floret staminate, or lacking stamens. Lemma of the sterile floret ovate to elliptic; 3.5 – 5 mm long; 1.3 – 1.8 mm wide; 5-nerved (rarely 7); the surface hairy; setose; acute; muticous. Palea of sterile floret fully developed; hyaline. Fertile floret 0.7 – 0.9 × the length of the sterile floret. Lemma of fertile floret elliptic; 3.1 – 4.6 mm long; 5-nerved; acute to rounded; mucronate. Chromosome number $2n = 36$ (*Shaw 2158*). No report for var. *simpsonii*.

KEY TO THE VARIETIES OF MICHAUXII

Lower floret staminate; rachis and inflorescence branches usually pilose; leaf blades generally flat and greater than 8 mm wide ..... var. *michauxii*

Lower floret neuter; rachis and inflorescence branches scabrous or puberulent; leaf blades involute to conduplicate, less than 5 mm wide ..... var. *simpsonii*

ERIOCHLOA MICHAUXII var. MICHAUXII. Fig. 7.

Panicum molle Michx., Fl. Bor. Amer. 1:47. 1803, non *P. molle* Sw., 1788. *Eriochloa mollis* (Michx.) Kunth, Rev. Gram. 1:30. 1829.

Panicum michauxii Roem. & Schult., Syst. Veg. 2:427. 1817.

Panicum michauxianum Schult., Mantissa 2:227. 1824, based on *P. molle* Michx.

Panicum georgicum Spreng., Syst., Veg. 1:308. 1825.

Eriochloa mollis var. *longifolia* Vasey, Bull. Torrey Bot. Club 13:25. 1886. *Eriochloa longifolia* (Vasey) Vasey, Contr. U.S. Natl. Herb. 3:21. 1892.

Eriochloa debilis Mez., Bot. Jahrb. Syst. 56: Beibl. 125:12. 1921.

Habitat and distribution: Brackish or fresh water marshes, "hammocks" and prairies in southeastern South Carolina and Georgia and throughout Florida.

Representative specimens: UNITED STATES. **Florida**: **Alachua Co.**: Gainesville, *Silvens 40121* (US); pasture survey plots, UF, *West & Arnold s.n.* (FLAS). **Brevard Co.**: *Fredholm 6000* (NY, US); Titusville, *Chase 5011* (NY, US); near Juniper Inlet, *Curtiss 5556* (NY, US); Merritt Island, *Swallen 195* (US). **Carlotte Co.**: cabbage palm hammock, *Frye C-37* (FLAS). **Citrus Co.**: Homosassa, *Combs 985* (US). **Collier Co.**: 1 mi S of Collier - Hendry Co. N boundary, *Lakela 29180* (FLAS); grassy opening in low pineland, *Lakela*

27751 (FLAS). **Dixie Co.**: upper Steinhatcheee River, *Kral & Redfearn 3080* (NY). **Duval Co.**: near Jacksonville, *Curtiss 3600* (NY, US), *4038* (MO, NY), *5086* (MO, NY); St. John's River, *Kearney 159* (US). **Indian River Co.**: Vero, *Thompson 175* (FLAS). **Lafayette Co.**: Suwannee River, *Combs 883* (US). **Lee Co.**: Sanibel, *Hitchcock 463* (US), *464* (US); Sanibel Island, *Brumback 6456* (FLAS); low ground in water, Fort Meyers, *McWilliam s.n.* (FLAS); Captiva Island, *Brumbach 5788* (FLAS). **Levy Co.**: Gulf Hammock, *Garber s.n.* (FLAS); 1 mi SE of Rosewood, no name (FLAS). **Madison Co.**: Ellaville, *Godfrey, Kral & Gillespie 53940* (NY). **Manatee Co.**: Terra Coca Island, *Cuthbert 1447* (FLAS); dunes, Anna Maria Key, *Cuthbert s.n.* (FLAS). **Monroe Co.**: Big Pine Key, *Killip 40933* (US); Palm Key, *Tracy 7373* (NY). **Pinellas Co.**: Mullet Key, Fort De Soto Park, *Lakela 26531* (FLAS, US). **St. Johns Co.**: moist ground, San Augustine, *Curtiss 6252* (FLAS). **Sarasota Co.**: Keys, *Garber s.n.* (FLAS). **Suwanee Co.**: moist bank of Suwannee River, *McDaniel 9452* (FLAS); no locality, *Hitchcock* in 1898 (US). **Volusia Co.**: low flatwoods, *Hood 24273* (FLAS). **Wakulla Co.**: NW of St. Marks, *Harper 215* (NY). **Georgia. Charlton Co.**: NE of Folkston, *Harper 1515* (NO, NY, US). **Glynn Co.**: E side of St. Simons Island, *Duncan & Duncan 29639* (FLAS, VDB). **South Carolina. Beaufort Co.**: Hilton Head Forest Beach, *Swank 1343* (USF).

ERIOCHLOA MICHAUXII var. SIMPSONII Hitchc., Proc. Biol. Soc. Wash. 41:163. 1928. TYPE: UNITED STATES. FLORIDA. Collier Co.: Cape Romano, *Simpson 262* (HOLOTYPE: US!; ISOTYPES: NY!, US!).

Intermediate plants between the two varieties have been collected in Lee Co. (*Hitchcock 462, 463, 464*) and Monroe Co. (*Curtiss 15090*) Florida. The best character for delineation of the varieties is the absence of a staminate lower floret in *E. michauxii* var. *simpsonii*. Plants with long, flat and narrow leaf blades and with few inflorescence branches have been referred to as *E. longifolia* (Vasey) Vasey, but these characters vary considerably within *E. michauxii* var. *michauxii* and no taxonomic status is warranted for the narrow-leaved forms.

Habitat and distribution: Rare in low wet areas, roadsides or in washed sand and shell. Reported only from southwestern Florida.

Representative specimens: UNITED STATES. Florida. Lee Co.: no locality, *Eaton 1300* (NY, US); Sanibel Island, *Bumbach 5334* (NLU), *5583* (USF); Bonita Springs, *Lakela 27094* (USF). **Monroe Co.**: Flamingo, *Eaton 1354 1/1* (NY, US); Cape Sable, *Simpson 165* (NY, US); lower Matecumbe Key, *Swallen 5204* (US); Keys, *Swallen 4057* (TAES).

ERIOCHLOA NELSONII Scribner & Smith, U.S.D.A. Div. Agrostol. Bull. 4:12. 1897. TYPE: MEXICO. OAXACA: Hills E of Cuicatlan, *Nelson 1707* (HOLOTYPE: US!; ISOTYPE: K!).

Plants annual. Cataphylls absent. Flowering culms 3 – 15 dm tall; erect or decumbent; rooting or not rooting at the lower nodes; 2 – 5-noded. Nodes hairy. Internodes hairy; pubescent. Sheaths not overlapping; not inflated; chartaceous; 35 – 150 mm long; smooth; hairy; pilose. Ligule a fringe of hairs; 0.3 – 1.5 mm long. Leaf blades linear; flat; straight;

spreading; 7 – 19 cm long; 5 – 17 mm wide; adaxially smooth; hairy on the adaxial surface. Prophyllum 30 – 50 mm long. Peduncle 150 – 450 mm long; hairy. Inflorescence 15 – 40 mm wide. Main axis 60 – 120 mm long; hairy. Primary branches spreading; 3 – 7 on the main axis (1 – 10); 12 – 35 mm long; 0.5 – 0.7 mm wide; not winged; hairy; pilose; with neatly arranged spikelets. Pedicels 0.5 – 1.5 mm long; hairy; with hairy apices (the hairs 3 – 8 mm long). Spikelets 14 – 40 on a typical primary branch; paired; divergent from the axis; lanceolate; 5 – 8 mm long; 1.5 – 2 mm wide. First glume absent. Second glume 1 × the length of the lower floret; lanceolate; 5, 7, or 9-nerved; hairy (becoming glabrous on the upper part); acute to obtuse; muticous. Sterile floret lacking stamens. Lemma of the sterile floret lanceolate; 4.8 – 7.8 mm long; 1.5 – 2 mm wide; 5-nerved (rarely 7); the surface hairy (becoming glabrous towards the apex); setose; acute; muticous. Palea of sterile floret vestigial, or absent; hyaline. Fertile floret 0.6 – 0.8 × the length of the sterile floret. Lemma of fertile floret elliptic; 3.2 – 4.4 mm long; 5-nerved; acute to rounded; mucronate (minute). Chromosome number $2n = 36$ for the typical variety (*Reeder & Reeder 6379*) and $2n = 72$ for var. *papillosa* (*Reeder & Reeder 6361*).

KEY TO THE VARIETIES OF NELSONII

Lemma and palea of fertile floret faintly rugose, shiny; spikelets 6 – 8 mm long ..... var. *nelsonii*

Lemma and palea of fertile floret coarsely rugose, dull; spikelets less than 6.0 mm long ..... var. *papillosa*

ERIOCHLOA NELSONII var. NELSONII. Fig. 8.

This is the only taxon of *Eriochloa* in North America that does not have numerous papillae in longitudinal and transverse rows covering the entire outer surface of the upper lemma and palea. In specimens examined with scanning electron microscopy (Shaw & Smeins 1981), the palea had only a few simple papillae scattered at the very tip, otherwise it was void of surface ornamentation.

Habitat and distribution: Weed along roadsides, in fields and other disturbed places, also in wet tropical deciduous forest, thorn savannas and on steep rocky slopes and hillsides at elevations of 200 – 2000 m from central Mexico southward to Guatemala, Honduras, and Nicaragua.

Representative specimens: **GUATEMALA. Chiquimula**: near village of Sasmo about 1 mi NW of Chiquimula, *Steyermark 30207* (F, US); above El Rincon, *Standley 74641* (F). **Escuintla**. no locality, *Aguilar 1683*. **Jutiapas**: between Jutiapa and La Calera, *Standley 76118* (F, US); vicinity of Jutiapa, *Standley 75399* (F). **HONDURAS. Choluteca**: San Antonio de Padua, *Standley 24675* (F). **MEXICO. Chiapas**: 9 km N of Tuxtla Gutierrez along the road to El Sumidero, *Breedlove 13882* (ENCB, F, MICH, TAES); 5 km E of

Fig. 8. *Eriochloa nelsonii* Scribner & Smith var. *nelsonii* (*Koch 77314*): A. Habit (× 1/2); B. Portion of inflorescence branch (× 3); C. Spikelet (× 6); D. Upper floret (× 6); E. Ligule (× 4).

Berriozabal along Mexican Hwy 190, *Breedlove 20410* (TAES); 5 km N of Tuxtla Gutierrez along the road to El Sumidero, *Breedlove & Raven 13537* (ENCB, F, MICH, TAES). **Colima**: 5 mi E of Colima on MEX 110, *Harvey & Witherspoon 93841* (MICH). **Guerrero**: 26 mi S of Chilpancingo, *Gould 10351* (MICH, TAES); Chacamerite, *Hinton 6943* (NY); Balsas, *Hitchcock 298* (F, NY); alre dedores de la salida del Rio Chontalcoatlan, *Quintero 1767* (ENCB, MICH); 10 km al N de Agua de Obispo, *Rzedowski 26895* (ENCB, MICH). **Jalisco**: 10 mi E of El Grullo, *Reeder & Reeder 6379* (ENCB, US); 1 km E de Mata de Bule cerca de Los Corales, *Rzedowski 17487* (ENCB, MICH). **Mexico**: Rincon del Carmen, *Hinton 1941* (NY); Villa Neda, Temancaltepec, *Hinton 6753* (MO, NY). **Michoacan**: Trixantla-Tiquicheo, *Hinton 13326* (NY); Ajuage, Apatzingan, *Hinton 15195* (NY). **Morelos**: lava fields near Yautepec, *Pringle 11224* (F, MO, NY, US). **Oaxaca**: from Temascalapa to San Ildefonso de Villa Alta, *Santos 3555* (MICH, NY, US). **NICARAGUA. Esteli**: in thickets of Estanzuela creek, 8 km W of Esteli, *Molina 23066* (F, MO); along railway, Catarina, *Hitchcock 8734* (MICH, US).

ERIOCHLOA NELSONII var. PAPILLOSA R.B. Shaw in R. McVaugh, Fl. Novo-Galiciana 78: 1982. TYPE: MEXICO. JALISCO. dry shaded ledges, bluffs of Rio Grande de Santiago near Guadalajara, 23 Sep 1889, *Pringle 2317* (HOLOTYPE: NY!; ISOTYPES: MO!, NY!, US!).

This variety appears intermediate between *E. nelsonii* and *E. lemmonii* and could be the result of hybridization between the two taxa. *Eriochloa nelsonii* var. *papillosa* is distributed at the northern most part of the range of *Eriochloa nelsonii*; however, it is not sympatric with *E. lemmonii* which has not been reported farther south than southern Chihuahua and Sonora.

Habitat and distribution: Growing on rocky steep slopes in forested areas or in open grasslands. Fairly abundant in central Mexico (Jalisco, Michoacan and Nayarit). All specimens reported at elevations greater than 1000 m.

Representative specimens: MEXICO. **Guerrero**: no locality, *Iltis & Doebly 317* (MO). **Jalisco**: road to Colima 13 km S of Tuxpan, *Burch 5159* (MO); near Rio Grande de Santiago, 27 km N of Guadalajara, *Leavenworth & Leavenworth 1895* (MO, US); near El Molina, about 25 mi SW of Guadalajara, *McVaugh 13295* (MICH, US); Barranca of Rio Verde, ca 20 mi N of Tepatitlan on road to Yahualica, *McVaugh 7430* (ENCB, MICH, NY, US); above Ahuacapan, road to Corralitos, ca 10 mi SSE of Autlan, *McVaugh 19536* (MICH, NY, US); mountains N of Autlan 305 mi above Mina San Francisco, *McVaugh 19708* (MICH); 48 mi SW of Suhauyo on Hwy 110, *Pratt 688* (TAES); ledges, barranca near Guadalajara, *Pringle 4047* (NY); 3 mi NW of Tequila, *Reeder & Reeder 2396* (ENCB); ca 5 mi SSW of Atenquique, *Reeder & Reeder 6361* (ENCB); 14 mi NW of Magdalena, *Waterfall 16351* (MICH, US). **Michoacan**: Coalcoman, *Hinton 12141* (F, NY, US); Cerro de Carboneras above the Rio Cupatitzio, ca 22 km S of Uruapan, *King & Soderstrom 4908* (MICH, NY). **Nayarit**: Rincon de Mateo, near Yxtlan, *Mexia 783-A* (F, MICH, MO, NY, US).

ERIOCHLOA PACIFICA Mez, Bot. Jahrb. Syst. 56(Beibl. 125):11. 1921. TYPE: ECUADOR. Puna Islands, *Eggers 14772* (LECTOTYPE: US!).

Plants annual. Cataphylls absent. Flowering culms 3—9 dm tall; erect

or decumbent; rooting or not rooting at the lower nodes; 2 – 5-noded. Nodes hairy. Internodes glabrous (or with a few hairs at the apex). Sheaths not overlapping; not inflated; chartaceous; 30 – 80 mm long; smooth; glabrous. Ligule a fringe of hairs; 0.7 – 1.5 mm long. Leaf blades filiform to lanceolate; flat or conduplicate; flexuous; spreading; 5 – 20 cm long; 3 – 12 mm wide; adaxially smooth; hairy on the adaxial surface. Prophyllum 30 – 60 mm long. Peduncle 40 – 100 mm long; glabrous. Inflorescence 10 – 40 mm wide. Main axis 30 – 120 mm long; hairy. Primary branches appressed to the main axis to spreading; 4 – 16 on the main axis; 15 – 25 mm long; 0.3 – 0.5 mm wide; not winged; hairy; setose; with loosely arranged spikelets. Pedicels 0.5 – 1.5 mm long; hairy; with hairy apices (terminal hairs 2 – 6 mm long). Spikelets paired (becoming solitary towards the apex); not divergent from the axis; lanceolate; 5 – 7 mm long; 0.9 – 1.2 mm wide. First glume absent. Second glume 1.1 – 1.2 × the length of the lower floret; lanceolate; 5-nerved; hairy (glabrous towards the apex); acuminate; muticous. Sterile floret lacking stamens. Lemma of the sterile floret lanceolate; 4 – 6 mm long; 0.9 – 1.2 mm wide; 5-nerved; the surface hairy; setose; acuminate; muticous. Palea of sterile floret absent. Fertile floret 0.58 – 0.7 × the length of the sterile floret. Lemma of fertile floret elliptic; 2 – 2.5 mm long; 5-nerved; acute to rounded; awned. Lemma of fertile floret awn 0.2 – 0.5 mm long. Chromosome number unknown.

Habitat and distribution: Wet and sandy areas, coastal marshes, grasslands and playas in Ecuador (including the Galapagos Islands) and Peru. Adventive in Central America and may not be a permanent member of the flora.

Representative specimens: NICARAGUA. Corinto, *Hitchcock 8749* (US).

ERIOCHLOA POLYSTACHYA Kunth, Nov. Gen. et Sp. 1:95, pl. 31. 1816.

Fig. 9. TYPE: ECUADOR. crescit in pascius inundatis prope Guayaquil, Regno Quit. (HOLOTYPE: B). *Milium polystachyon* (Kunth) Spreng., Syst. Veg. 1:252. 1825. *Helopus polystachyus* (Kunth) Trin. ex Steud., Nom. Bot. ed. 2, 1:747. 1840.

Monachne subglabra Nash, Bull. Torrey Bot. Club 30:374. 1903. *Eriochloa punctata* (L.) Desv. ex Hamilt. var. *subglabra* (Nash) Urban, Symb. Antill. 4:85. 1903. *Eriochloa subglabra* (Nash) Hitchc., Contr. U.S. Natl. Herb. 12:208. 1909.

Plants perennial; lacking rhizomes. Flowering culms 10 – 20 dm tall (total length); decumbent; rooting at the lower nodes; 4 – 10-noded. Nodes hairy. Internodes glabrous. Sheaths overlapping or not overlapping; not inflated; chartaceous to chartilaginous; 40 – 80 mm long; smooth; glabrous (the lower ones hairy). Ligule a fringe of hairs (with a minute membranous part about 0.2 mm long at the base); 0.6 – 1.2 mm long.

Collar hairy. Leaf blades linear; flat; straight; spreading; 6 – 28 cm long; 6 – 18 mm wide; adaxially smooth; glabrous on the adaxial surface. Prophyllum 60 – 90 mm long. Peduncle 150 – 340 mm long; hairy. Inflorescence 41 – 90 mm wide. Main axis 80 – 200 mm long; hairy. Primary branches spreading; 10 – 15 on the main axis (5 – 18); 20 – 60 mm long; 0.4 – 0.6 mm wide; not winged; hairy; pubescent to setose; with loosely arranged spikelets. Pedicels 0.5 – 1 mm long; glabrous or hairy; with glabrous apices. Spikelets paired; not divergent from the axis; lanceolate to ovate; 3.2 – 3.9 mm long; 1.1 – 1.3 mm wide. First glume present. Second glume 1 × the length of the lower floret; lanceolate to ovate; 5-nerved; hairy; acute; muticous. Sterile floret staminate or lacking stamens. Lemma of the sterile floret lanceolate to ovate; 3 – 3.5 mm long; 1.1 – 1.3 mm wide; 5-nerved; the surface hairy; setose to pilose; acute; muticous. Palea of sterile floret fully developed, or absent; hyaline. Fertile floret 0.6 – 0.8 × the length of the sterile floret. Lemma of fertile floret elliptic; 2.2 – 2.6 mm long; rounded; mucronate (the mucro less than 0.2 mm long). Chromosome number $2n = 36$ (de Wet 1960; Pohl & Davidse 1971).

Habitat and distribution: Coastal marshes, swamps, ditches and moist ground from the West Indies, Costa Rica and Honduras to South America (Brazil, Ecuador, Colombia, Guyana, Peru, Surinam, Venezuela). Introduced into Florida, Mississippi and Texas as a forage crop.

Representative specimens: **COSTA RICA. Alajuela**: near La Laguna, *Molina, Williams, Burger & Wallenta 17468* (F). **Puntarenas**: 4 km E of San Vito de Java, *Pohl & Davidse 10782* (F). **Limon**: 21 km SW of Siquirres, *Pohl & Davidse 10849* (F). **CUBA**: no locality, *Wright 1545* (NY). **HONDURAS: Cortez**: vicinity of La Lima, *Standley & Chacon 7105* (F). **JAMAICA**: Meyersfield, *Adams 10154* (MO). **PUERTO RICO**: between Ponce and Santa Isabel, *Britton & Brown 5513* (MO); Rio Piedras, *Chase 6360* (MO); near Bayamon, *Liogier 10321* (NY); near Lares, *Liogier 9953* (NY); Rio Piedras, *Otero 238* (MICH); Carolina, *Sargent 580* (MICH). **TRINIDAD**: St. Anns, *Broadway 7784* (MO); SW of Arima, *Davidse 2537* (MO).

UNITED STATES. **Florida**: **Alachua Co.**: Williamson Tract, *Killinger s.n.* (FLAS). **Indian River Co.**: Fellsmere, *Tracy 2889.2* (TAES). **Pasco Co.**: pasture, *Smith s.n.* (FLAS). **Mississippi**: **Harrison Co.**: Biloxi, *Tracy 38030* (TAES). **Texas**: **Brazoria Co.**: Angleton, *Nees* in 1926 (TAES).

ERIOCHLOA PSEUDOACROTRICHA (Stapf ex Thell.) C.E. Hubb. ex S.T. Blake, Trans. & Proc. Roy. Soc. South Australia 67:43. 1943. *Eriochloa ramosa* (Retz.) Kuntze var. *pseudoacrotricha* Stapf ex Thell. TYPE: AUSTRALIA. (HOLOTYPE: K!).

E. annulata (Fluegge) Kunth var. *acrotricha* (Steud.) Benth., non *Helopus acrotrichus* Steud., 1840.

Plants perennial; lacking rhizomes. Cataphylls present. Flowering

Fig. 9. *Eriochloa polystachya* Kunth (*Tracy 38892*): A. Habit (× 1/2); B. Portion of inflorescence branch (× 6); C. Spikelet (× 12); D. Upper floret (× 12); E. Ligule (× 2).

culms 4 – 8 dm tall; erect; not rooting at the lower nodes; 2 – 5-noded. Nodes hairy. Internodes glabrous. Sheaths not overlapping; not inflated; chartaceous; 30 – 100 mm long; smooth; glabrous (rarely with a few appressed hairs). Ligule a fringe of hairs; 0.4 – 1 mm long. Collar glabrous. Leaf blades linear; flat; straight; spreading; 10 – 20 cm long; 2 – 4 mm wide; adaxially smooth; glabrous; or hairy on the adaxial surface. Prophyllum 30 – 50 mm long. Peduncle 100 – 300 mm long; glabrous. Inflorescence 3 – 10 mm wide. Main axis 50 – 150 mm long; scabrous. Primary branches appressed to the main axis to spreading; 2 – 8 on the main axis; 25 – 45 mm long; 0.3 – 0.6 mm wide; winged; glabrous; with loosely arranged spikelets. Pedicels 1 – 3 mm long; glabrous; with hairy apices. Spikelets 20 – 40 on a typical primary branch; paired (becoming solitary at the branch apex); not divergent from the axis; lanceolate; 3.6 – 5.4 mm long; 1.1 – 1.4 mm wide. First glume absent. Second glume 1 – 1.3 × the length of the lower floret; lanceolate; 5-nerved; hairy; acuminate; awned. Second glume awn 0.5 – 1.5 mm long. Sterile floret lacking stamens. Lemma of the sterile floret lanceolate; 3.5 – 5.2 mm long; 1.1 – 1.4 mm wide; 5-nerved; the surface hairy; setose; mucronate to awned. Palea of sterile floret absent. Fertile floret 0.6 – 0.8 × the length of the sterile floret. Lemma of fertile floret elliptic; 2.1 – 3.7 mm long; rounded; awned. Lemma of fertile floret awn 0.4 – 0.8 mm long. Chromosome number $2n = 36$ (Nath et al. 1970).

Habitat and distribution: Roadsides, ditches and creek margins in Australia (Queensland, New South Wales, South Australia). Introduced (probably accidentally) into south Texas.

Representative specimens: UNITED STATES. **Texas**: **Cameron Co.**: 7 mi S of San Benito, Hwy 281, *True s.n.* (US); waste lot near railroad, San Benito, *Runyon 1882* (US). **Kenedy Co.**: S of Norias, *Swallen 10111* (US). **Kleberg Co.**: Hwy 141, W of Kingsville, *Swallen 10251* (US).

ERIOCHLOA PUNCTATA (L.) Desv. ex Hamilt., Prodr. Pl. Ind. Occid. 5. 1825. Fig. 10. *Milium punctatum* L., Syst. Nat., ed. 10. 2:872. 1759. TYPE: JAMAICA. insula Americae Jamaica, *Browne s.n.* (HOLOTYPE: L). *Agrostis punctata* (L.) Lam., Encycl. 1:58. 1783. *Paspalum punctatum* (L.) Fluegge, Monogr. Pasp. 127. 1810. *Piptatherum punctatum* (L.) Beauv., Ess. Agrost. 18:168, 173, pl. 5, f. 11. 1812. *Oediptachne punctata* (L.) Link, hort. Berol. 1:51. 1827. *Helopus punctatus* (L.) Nees, Agrost. Bras. 16. 1829. *Monachne punctata* (L.) Nash, Bull. Torrey Bot. Club 30:374. 1903. *Eriochloa polystachya* Kunth var. *punctata* (L.) Maid. & Betche, Cens. N.S.W. pl. 16. 1916.

Eriochloa kunthii G. Meyer, Prim. Fl. Esseq. 46. 1818. *Helopus kunthii* (G. Meyer) Trin. ex Steud., Nom. Bot., 1(2):747. 1840.

Plants perennial (often flowering the first year and giving the appearance

of an annual); rhizomatous (frequently absent on herbariumn specimens). Cataphylls present. Flowering culms 3 – 15 dm tall; erect or decumbent; not rooting at the lower nodes; 3 – 10-noded. Nodes hairy or glabrous. Internodes glabrous. Sheaths not overlapping; not inflated; chartaceous; 60 – 110 mm long; smooth; glabrous (rarely puberulent). Ligule a fringe

Fig. 10. *Eriochloa punctata* (L.) Desv. ex Hamilt. (*Beetle M-1184*): A. Habit (× 1/2); B. Portion of inflorescence branch (× 5); C. Spikelet (× 12); D. Upper floret (× 12); E. Ligule (× 2).

of hairs; 0.4 – 1 mm long. Leaf blades linear; flat; straight; spreading; 10 – 50 cm long; 4 – 10 mm wide (2 – 13); adaxially smooth; glabrous or hairy on the adaxial surface. Prophyllum 40 – 80 mm long. Peduncle 200 – 450 mm long; glabrous or hairy. Inflorescence 10 – 100 mm wide. Main axis 90 – 220 mm long; scabrous to hairy. Primary branches appressed to the main axis, or spreading; 8 – 20 on the main axis (4 – 27); 10 – 60 mm long; 0.3 – 0.5 mm wide; not winged; glabrous; with loosely arranged spikelets. Pedicels 0.1 – 0.7 mm long; glabrous (rarely with a few scattered hairs); with glabrous apices. Spikelets 28 – 60 on a typical primary branch; paired (becoming solitary towards the apex); not divergent from the axis; (4.0 –) 4.5 – 5.7 mm long; 0.9 – 1.4 mm wide. First glume absent. Second glume 1 × the length of the lower floret; lanceolate; 5 – 7-nerved; hairy; acuminate; muticous (or slightly mucronate). Sterile floret lacking stamens. Lemma of the sterile floret lanceolate; 4.3 – 5.5 mm long; 0.9 – 1.4 mm wide; 5 – 7-nerved; the surface hairy; setose; acuminate; muticous to mucronate. Palea of sterile floret absent. Fertile floret 0.5 – 0.6 × the length of the sterile floret. Lemma of fertile floret elliptic; 2 – 3.5 mm long (excluding the awn); 5-nerved; rounded; awned. Lemma of fertile floret awn 0.6 – 1.5 mm long. Chromosome number $2n = 36$ (Gould 1966; Gould & Soderstrom 1967).

Habitat and distribution: In coastal marshes, along water courses, moist swales, and ditches. Occurring from southwestern Louisiana, along the coastal plains of Texas, Mexico, Belize, Nicaragua, Panama, Costa Rica, Cuba, Puerto Rico to South America (Brazil, Ecuador, Guyana, Peru, Bolivia, Argentina, Paraguay, Uruguay, Colombia, Surinam and Venezuela).

Representative specimens: **ANTIGUA**: no locality *Hitchcock 16387* (US). **BELIZE**: Sibun River, *Gentle 8425* (F, NY, US); Humming Bird Hwy, *Gentle 8875* (F); near Aerodrome, *Smart 76* (US). **COSTA RICA. San Jose**: edge of Pejibaye, *Molina, Burger & Wallenta 18257* (F). **Limon**: Rio Coen, *Ocampo 1838* (US); Pandora, *Ocampo 1973* (US). **CUBA. Habana**: near Guanabacoa, *Ekman 13172* (MICH, NY); near Luyano, *Leon 4217* (NY). **Oriente**: Baracoa, *Ekman 4010* (NY); no locality, *Wright 1542* (US). **DOMINICAN REPUBLIC**: along Nizao River, *Allard 17023* (US). **GUATEMALA. Izabal**: Puerto Barrios, *Standley 24800* (US), *Hitchcock 9156* (MICH, US). **Peten**: along Rio Caucuen, *Steyermark 45941* (F, MICH, US); near Quirigua, *Weatherwax 1547* (MO). **HAITI**: Fond-des-Negres, *Ekman H7161* (US). **JAMAICA**: Appleton, *Hitchcock 9661* (MO); vicinity of Windsor, *Maxon & Killip 269* (NY). **MARTINIQUE:** no locality, *Duss 4027* (NY). **MEXICO. Chiapas**: Pugiltic, *Breedlove 10032* (ENCB); Comitan, *Matuda 15802* (F); Palenque, *Matuda 3759* (F, MICH, NY); Tenejapa, *Ton 1670* (ENCB, F). **Coahuila**: Monclova, *Harvey 1147* (MICH, MO). **Guerrero**: San Miguel, *Hinton 5671* (NY); Santa Barbara, *Hinton 5648* (NY); Pungarabato, *Hinton 6007* (NY). **Tabasco**: Tenosique, *Matuda 3431* (F, MICH, NY). **Tamaulipas**: Hacienda Santa en Gracia, *Chase 7590* (MICH); 13 mi N of Mante, *Gould 7007* (MICH, TAES). **Vera Cruz**: 19 mi SE of

Jalapa, *Gould 11714* (TAES); la Esperanza, *Ventura 10970* (ENCB); Paso la Milpa, *Ventura 3192* (ENCB); Los Reyes, *Ventura 3492* (ENCB, MICH); Fortuno, *Williams 8261* (F, MICH). **MONTSERRAT**: Shafer 536 (NY). **ST. CROIX**: St. John Estate, *Ricksecker 467* (NY). **NICARAGUA. Zelaya**: Rio Grande, *Molina 2351* (F, NY, US). **PANAMA**: Laguna de Chiriqui, *Hart 64* (US). Darien: along Sambu River, *Pittier 5529* (US). **PUERTO RICO**: 8 mi from Pounce, *Heller 6298* (NY); Rio Piedras, *Molinari* in 1941 (TAES); no locality, *Sintenis 4253* (MO, NY). **TORTOLA**: *Britton & Shafer 761* (NY); *Fishlock 107* (NY). **TRINIDAD**: Cedros, *Hitchcock 10141* (US).

UNITED STATES. **Louisiana: Cameron Parish**: Cameron, *Tracy 8594* (NY, TAES); Little Chenier, E of Creole, *Brown 19945* (NLU), *Brown 9243* (LSU), *Chamberlain E5C5-5* (LSU), *Thomas 48237* (NLU). **Texas**: **Cameron Co.**: Harlingen, *Tharp 1782* (US); Brownsville, *Swallen 1347* (US), *1409* (US), *1435* (US), *1485* (US), *Hitchcock 5403* (US). **Galveston Co.**: Galveston Island, *Tracy 7407* (NY); San Leon, *Waller & Bauml 3019* (TAES). **Hidalgo Co.**: 2 mi S of Parr, *Gould 13998* (TAES). **Jim Wells Co.**: N of Alice, *Silveus 7425* (TAES). **Victoria Co.**: Victoria, *Plank 75* (US). **San Patricio Co.**: 5 mi SW of Mathis, *Gould 11463* (TAES). **Starr Co.**: Rio Grande City, *Swallen 1565* (US), 1567 (US), *Griffiths 6489* (US). **Willacy Co.**: *Cory 51478* (NY).

ERIOCHLOA SERICEA (Scheele) Munro ex Vasey, U.S.D.A. Div. Bot. Bull. 12: pl. 1. 1890. Fig. 11. *Paspalum sericeum* Scheele, Linnaea 22:341. 1849. TYPE: UNITED STATES. TEXAS. Comal Co.: An feuchten Stellen bei Neubranfels, *Lindheimer 556* (HOLOTYPE: K!; ISOTYPES: MO!, NY!, US!). *Panicum sericatum* (Scheele) ex Steud., Syn. Pl. Glum. 1:58. 1854.

Paspalum racemosum Nutt., Trans. Amer. Phil. Soc. 5:145. 1837, non *P. racemosum* Lam., 1791.

Helopus junceus C. Muell., Bot. Zeitung (Berlin) 19:314. 1861.

Plants perennial; rhizomatous (with compacted internodes producing a bunchgrass appearance). Cataphylls present. Flowering culms 3 – 13 dm tall; erect or decumbent; rooting or not rooting at the lower nodes; 2 – 5-noded. Nodes hairy. Internodes hairy; pubescent. Sheaths not overlapping; not inflated; chartaceous; 30 – 140 mm long; smooth; glabrous or hairy; pubescent. Ligule a fringe of hairs; 0.5 – 1.5 mm long. Leaf blades filiform to linear; involute (occasionally flat); straight to flexuous; appressed to the culm to spreading; 10 – 30 cm long; 0.5 – 4 mm wide; adaxially smooth; glabrous, or hairy on the adaxial surface. Peduncle 100 – 250 mm long; glabrous, or hairy. Inflorescence 5 – 15 mm wide. Main axis 40 – 200 mm long; hairy. Primary branches appressed to the main axis; 4 – 8 on the main axis (2 – 10); 10 – 35 mm long; 0.4 – 0.7 mm wide; winged; or not winged; hairy; velutinous; with neatly arranged spikelets. Pedicels 0.4 – 0.7 mm long; hairy; with hairy apices. Spikelets 10 – 20 on a typical primary branch; solitary; not divergent from the axis; 4 – 5 mm long; 1.4 – 1.9 mm wide. First glume absent. Second glume ovate to elliptic; 5 – 7-nerved; hairy; acute; muticous. Sterile floret lacking stamens. Lemma of the sterile floret elliptic; 3.8 – 4.8 mm long; 1.5 – 1.9 mm

wide; 5 − 7-nerved; the surface hairy; pubescent to velutinous; acute; muticous. Palea of sterile floret absent. Fertile floret 0.7 − 0.8 × the length of the sterile floret. Lemma of fertile floret elliptic; 2.7 − 3.6 mm long; acute; mucronate (the mucro 0.1 − 0.2 mm long). Chromosome number $2n = 54$ (Brown 1950; Gould 1968; *Shaw 781, 981*).

Habitat and distribution: Usually found on clay or clay-loam soils in prairies, roadsides or protected areas. Widespread in the Blackland Prairie and Edwards Plateau and extending into the Coastal Prairie and Rolling Plains of Texas, also found in southern Oklahoma and one collection has been made in Mexico.

Representative specimens: MEXICO. **Coahuila**: ca 10 mi NW of Rancho Margareta headquarters, 75 mi NW of Sabinas, *Gould 10707* (ENCB, MICH, TAES)

UNITED STATES. **Oklahoma: Cotton Co.**: 15 mi S of Lawton, *Rose-Innes & Moon 979* (US). **Murray Co.**: about 0.5 mi W of Honey Creek, Arbuckle Mountains, *Robbins 3170* (TAES); Davis, *Emig 708* (MO, US). **Pottawatomie Co.**: Tecumseh, *Demaree 12529* (US). **Woodward Co.**: Southern Great Plains Field Station, *Savage 791* (US). **Texas**: **Atascosa Co.**: Pleasanton, *Swallen 17811* (US). **Bee Co.**: 11 mi NW of Sinton, *Gould 9512* (TAES). **Bell Co.**: 11.5 mi W of Rosebud, *Gould 8881* (TAES). **Bexar Co.**: Leon Springs, *Clemens & Clemens* in 1911 (MO). **Bosque Co.**: 10 mi N of Valley Mills on FM 56, *Terry 42* (TAES). **Brown Co.**: near Brownsville, *Swallen 1462* (US). **Comal Co.**: Comanche Springs, New Braunfels, *Lindheimer 1256* (MO, NY). **Cook Co.**: 8 mi N of Gainesville, *Whitehouse 15795* (NY). **Dallas Co.**: Blackland Prairies, *Reverchon 1170* (MO). **Denton Co.**: 2.5 mi S of Sanger, *Cory 53239* (NY). **Duval Co.**: San Diego, *Croft 233* (NY). **Hays Co.**: 7 mi W of San Marcos, *Gould 6689* (TAES). **Karnes Co.**: 0.6 mi NW of Kenedy on Hwy 181, *Johnson 1215* (TAES). **Kendall Co.**: Boerne, *Palmer 9797* (MO). **Kerr Co.**: Kerrville, *Smith* in 1897 (US). **Lampasas Co.**: Lampasas, *Wolff 5084* (TAES). **McClennan Co.**: 7 mi S of McGregor, *Henard 64-30* (TAES). **Nolan Co.**: near Blackwell, *Palmer 34578* (NY). **Shackelford Co.**: ca 3 mi W of Albany along U.S. 180, *Henderson 63-971* (TAES). **San Patricio Co.**: Welder Wildlife Refuge, *Gould 8598* (TAES). **Sterling Co.**: 8 mi N of Sterling, *Hitchcock 13392* (US). **Sutton Co.**: Texas Agriculture Experiment Station, 30 mi SE of Sonora, *Gould & Merrill 5762* (TAES). **Taylor Co.**: *Tolstead 7562* (TAES). **Throckmorton Co.**: 10 mi S of Throckmorton, *Fowler 63-51* (TAES). **Tom Greene Co.**: no locality, *Tweedy s.n.* (NY). **Travis Co.**: near Austin, *Swallen 1038* (US). **Uvalde Co.**: near Uvalde, *Palmer 11037* (US). **Williamson Co.**: 2.5 mi W of Georgetown, *Gould 5956* (TAES).

ERIOCHLOA SETOSA (A. Rich.) Hitchc., U.S.D.A. Misc. Publ. 243:182. 1936. *Piptatherum setosum* A. Rich. in Sagra, Hist. Cuba 11:311. 1850. TYPE: CUBA. crescit in locis siccis et incultis insulae Cubae (HOLOTYPE: P).

Plants perennial; lacking rhizomes. Cataphylls absent. Flowering culm 1 − 6 dm tall; erect; not rooting at the lower nodes; 3 − 7-noded. Nodes hairy. Internodes glabrous. Sheaths not overlapping; not inflated; chartaceous; 10 − 40 mm long; smooth; glabrous or hairy; pubescent. Ligule a fringe of hairs; 0.3 − 0.7 mm long. Leaf blades filiform; flat, or involute; straight to flexuous; spreading; 4 − 5 cm long; 0.5 − 2 mm wide;

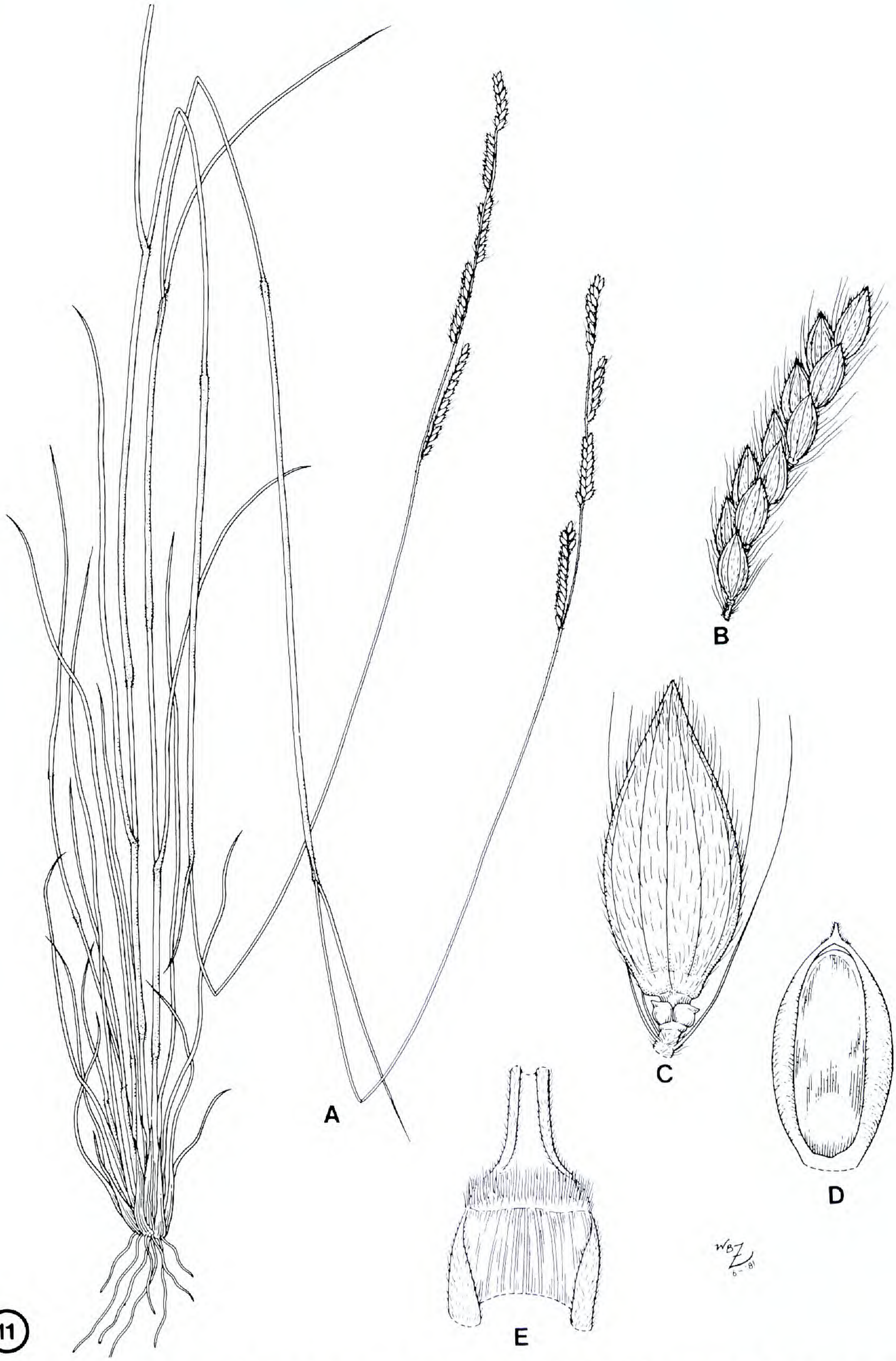

Fig. 11. *Eriochloa sericea* (Scheele) Munro ex Vasey (*Shaw 923*): A. Habit (× 1/2); B. Portion of inflorescence branch (× 3); C. Spikelet (× 12); D. Upper floret (× 12); E. Ligule (× 6).

adaxially smooth; glabrous; or hairy on the adaxial surface. Prophyllum 15 – 30 mm long. Peduncle 90 – 170 mm long; glabrous. Inflorescence 5 – 30 mm wide. Main axis 5 – 40 mm long; smooth (or with minute hairs or scabrosities). Primary branches spreading; 1 – 6 on the main axis; 12 – 15 mm long (6 – 20); 0.1 – 0.2 mm wide; not winged; glabrous; with loosely arranged spikelets. Pedicels 0.2 – 1 mm long; glabrous; with glabrous apices (occasionally with a few minute hairs). Spikelets 4 – 10 on a typical primary branch; solitary; not divergent from the axis; lanceolate; 3 – 4 mm long; 0.8 – 1 mm wide. First glume absent. Second glume 1.1 – 1.2 × the length of the lower floret; lanceolate; 5-nerved; hairy; acuminate; muticous; or awned. Second glume awn 0.3 – 0.7 mm long. Sterile floret lacking stamens. Lemma of the sterile floret lanceolate; 2.5 – 3.4 mm long; 0.8 – 1 mm wide; 5-nerved; the surface hairy; setose; acuminate; muticous. Palea of sterile floret absent. Fertile floret 0.6 – 0.7 × the length of the sterile floret. Lemma of fertile floret elliptic; 1.6 – 2.5 mm long; 5-nerved; rounded; awned. Lemma of fertile floret awn 0.2 – 1 mm long. Chromosome number unknown.

KEY TO THE VARIETIES OF SETOSA

Leaf blades involute and filiform; lemma of the upper floret with an awn 0.5 – 1.0 mm long ..... var. *setosa*

Leaf blades flat; lemma of the upper floret mucronate or with an awn less than 0.5 mm long ..... var. *ekmanii*

ERIOCHLOA SETOSA var. SETOSA. Fig. 12.

Eriochloa filifolia Hitchc., Contr. U.S. Natl. Herb. 12:207. 1909. TYPE: CUBA. Guanabacoa, *Hitchcock 23223* (HOLOTYPE: US!; ISOTYPE: NY!).

Habitat and distribution: On sandy or serpentine soils in wet savanna, hillsides and disturbed areas. Only reported to occur in Cuba.

Representative specimens: CUBA. **Camaguey**: Santayana, *Ekman 15331* (NY). **Habana**: near Buanabacoa, *Leon 1483* (NY); Loma de la Jata, *Wilson & Leon 11642* (NY); on Loma de las Jatas, *Ekman 13134* (MICH). **Matanzas**: San Miguel de los Bauos, *Leon & Roca 8856* (NY). **Santa Clara**: *Britton & Cowell 13288* (NY); Santa Clara, *Leon & Roca 8147* (NY); near Santa Rosalia Baths, *Leon & Loustalog 9380* (NY).

ERIOCHLOA SETOSA var. **ekmanii** (Hitchc.) R.B. Shaw, stat. et comb. nov.

Eriochloa ekmanii Hitchc., U.S.D.A. Misc. Publ. 243:183. 1936. TYPE: CUBA. ORIENTE: in savannas near Mir, 22 Aug 1916, *Ekman 7509* (HOLOTYPE: US! ISOTYPES: MICH!, NY!).

Habitat and distribution: in savannas, Cuba.

Representative specimens: CUBA. **Pinar del Rio**: Salado, Pinar de Barreto, *Ekman 11556* (MICH). **Camaguey**: Tiffin, *Ekman 15391* (US); Adelaida, *Leon 15804* (US). **Santa Clara**: Zaza de Tunas, *Leon 852* (US); no locality, *Wright 3886* (US).

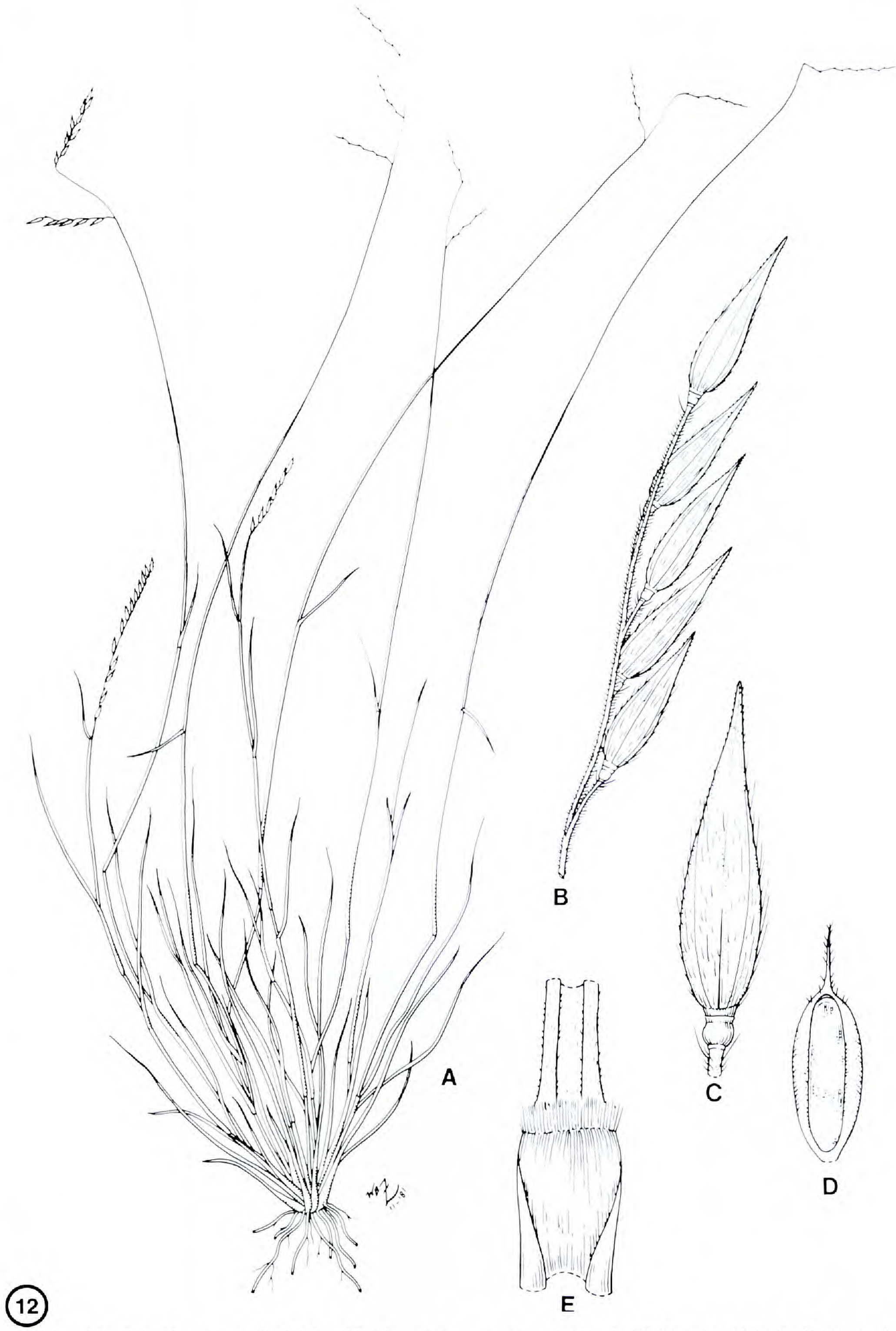

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Fig. 12. *Eriochloa setosa* (A. Rich.) Hitchc. var. *setosa* (*Leon 991*): A. Habit (× 1/2); B. Portion of inflorescence branch (× 6); C. Spikelet (× 12); D. Upper floret (× 12); E. Ligule (× 2).

ERIOCHLOA VILLOSA (Thunb.) Kunth, Rev. Gram. 1:30. 1829. Fig. 13.

Paspalum villosum Thunb., Fl. Jap. 45. 1784. TYPE: JAPAN. rescit iuxta Nagasaki (HOLOTYPE: B). *Helopus villosus* (Thunb.) Nees ex Steud., Nom Bot., 1(2):747. 1840.

Paspalum distichum Houtt., Natuurlyke Hist. Handleid. 13:167, pl. 89, fig. 4. 1782, non *Paspalum distichum* L., 1759.

Plants annual. Cataphylls absent. Flowering culms 3 – 10 dm tall; erect or decumbent; rooting or not rooting at the lower nodes; 2 – 5-noded. Nodes hairy. Internodes hairy; pubescent. Sheaths overlapping, or not overlapping; conspicuously inflated, or not inflated; chartaceous; 35 – 90 mm long; smooth; glabrous, or hairy; pubescent. Ligule a fringe of hairs; 0.5 – 1 mm long. Leaf blades linear to lanceolate; flat; straight to flexuous; spreading; 10 – 20 cm long; 5 – 12 mm wide; adaxially smooth; hairy on the adaxial surface. Prophyllum 20 – 45 mm long. Peduncle 100 – 300 mm long; hairy. Inflorescence 10 – 30 mm wide. Main axis 30 – 160 mm long; hairy. Primary branches appressed to the main axis to spreading; 2 – 8 on the main axis; 20 – 70 mm long; 0.8 – 1.1 mm wide; winged to not winged; hairy; pubescent and velutinous; with neatly arranged spikelets. Pedicels 0.5 – 1 mm long; hairy; with hairy apices. Spikelets 12 – 24 on a typical primary branch; solitary (rarely paired at the base); not divergent from the axis; ovate to elliptic; 3.9 – 5.2 mm long; 2 – 2.5 mm wide. First glume absent (occasionally represented by a scale). Second glume 1 × the length of the lower floret; ovate to elliptic; 7-nerved; glabrous, or hairy; acute; muticous. Sterile floret lacking stamens. Lemma of the sterile floret ovate to elliptic; 3.4 – 5 mm long; 2 – 2.5 mm wide; 5-nerved; the surface glabrous, or hairy; puberulent to pubescent; acute; muticous. Palea of sterile floret absent. Fertile floret 0.85 – 0.95 × the length of the sterile floret. Lemma of fertile floret ovate to elliptic; 3.5 – 5 mm long; acute; apiculate. Chromosome number $2n = 54$ (Tateoka 1954).

Habitat and distribution: Weed in fields and disturbed areas, native in eastern U.S.S.R., South and North Korea, Japan and China, introduced into the United States.

Representaive specimens: UNITED STATES. **Colorado**: **El Paso Co.**: Soil Erosion Experiment Station, *Silvens 2142* (TAES). **Florida**: **Alachua Co.**: test plots, *Thompson 335* (FLAS). **Mississippi**: **Harrison Co.**: Biloxi, *Tracy 01912* (TAES). **Illinois**: **Livingston Co.**: 3 mi E of Odell, 1950, *Meyers s.n.* (MO). **Wisconsin**: Racine, 1966, *Doersch s.n.* (MO, TAES).

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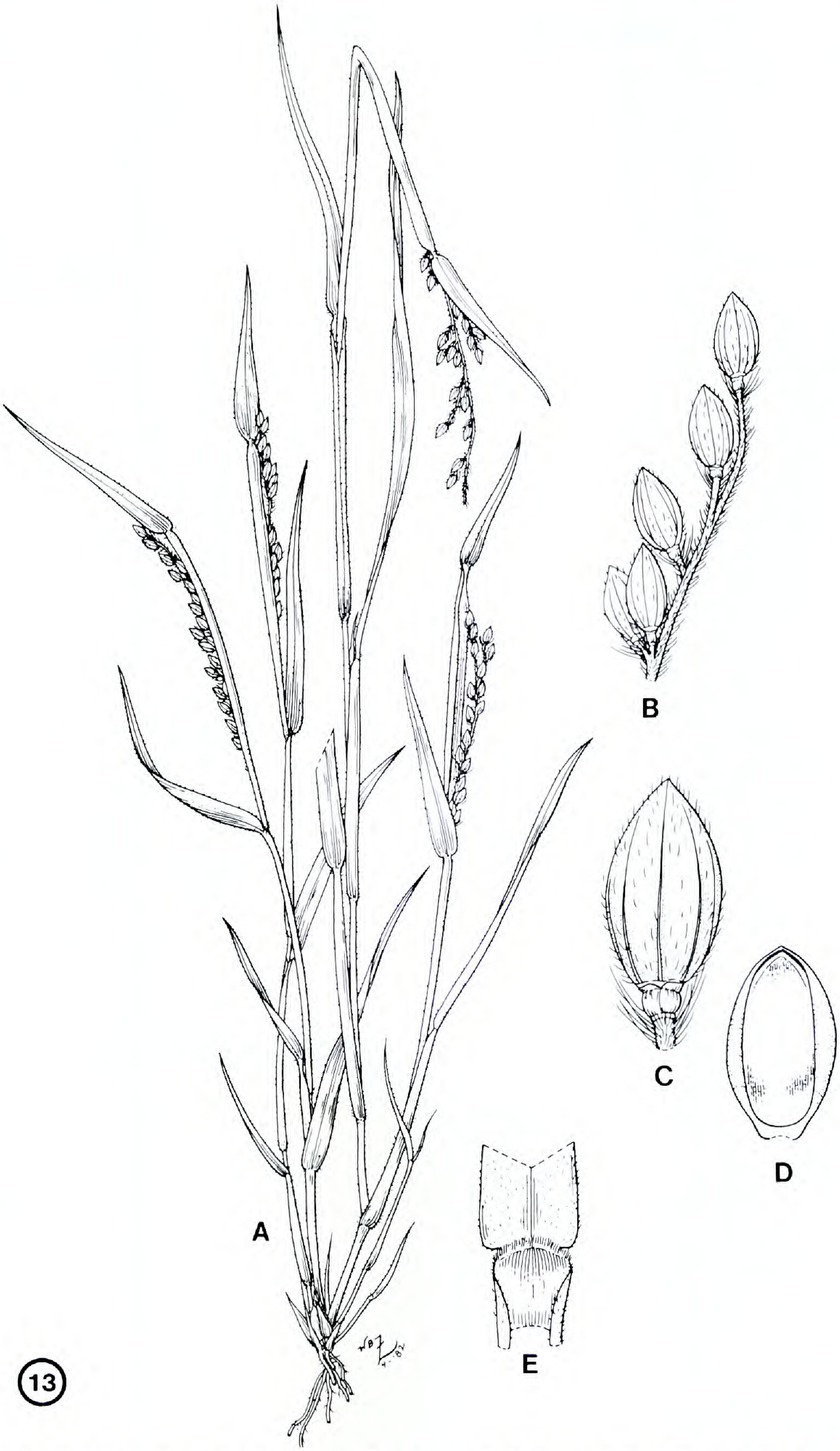

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Fig. 13. *Eriochloa villosa* (Thunb.) Kunth (*Doersch s.n.*): A. Habit (× 1/2); B. Portion of inflorescence branch (× 2); C. Spikelet (× 6); D. Upper floret (× 6); E. Ligule (× 3).

for interesting and helpful correspondence concerning the nomenclature of the genus. The curators of DUKE, ENCB, F, FLAS, G, K, LSU, MICH, MISS, MO, NCSD, NLU, NY, SMU, TAES, TENN, UARK, US, USF and VDB are gratefully acknowledged for the loan of herbarium specimens. Application of the DELTA system to the data in this study was funded by the USDA/ARS Beltsville, Maryland, where the programs are operational on PRIME and VAX computers.

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TAXONOMY OF *DIGITARIA* SECTION *DIGITARIA* IN NORTH AMERICA (POACEAE: PANICEAE)[1]

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ABSTRACT

Six species are recognized in a revision of *Digitaria* section *Digitaria* in North America. The taxonomy is based on phenetic and statistical analyses of 2,530 specimens from 245 populations. Recognized species include *D. bicornis, D. ciliaris, D. horizontalis, D. nuda, D. sanguinalis*, and *D. setigera*. The DELTA computer programs were used to produce the descriptions and key.

Henrard (1950), in his monograph of *Digitaria*, recognized 32 sections in the subgenus *Digitaria* (= *Eu-Digitaria*). Veldkamp (1973) merged the sections *Biformes* Henrard, *Horizontales* Henrard, *Sanguinales* (Stapf) Henrard and *Parviglumae* Henrard under the section *Digitaria*. This realignment was justified as members of these sections morphologically integrade (Webster 1981). Section *Digitaria* consists of annual species with paired spikelets occurring on winged primary branches. This section occurs in temperate to tropical regions throughout the world and is taxonomically a difficult group within a genus notorious for its morphological complexity. These species, commonly known as crabgrass, are noxious, weedy invaders of disturbed soil sites, and widely distributed in North America. In many areas, two or three species inhabit the same site, and it is not uncommon to find more than one species represented on a herbarium sheet. Taxonomists disagree on the classification of the taxa in the section. Henrard (1950) recognized numerous species, subspecies and varieties, whereas Hitchcock (1951) maintained a broad species concept. Authors in North America followed Hitchcock's concepts which did not account for much of the variation. The conflicting taxonomic systems produced by Henrard and Hitchcock were, in part, the result of taxonomic opinion, but also result from a lack of reliable information on the morphological relationships within and among natural populations.

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SIDA 12(1): 209–222. 1987.

The primary objective of this study is to present a revised taxonomic treatment of *Digitaria* section *Digitaria* in North America. A secondary objective is to illustrate the practical application of the DELTA computer system (Dallwitz 1980a & b). The descriptions and key presented here were produced from data coded in DELTA format. This system has been applied successfully to plants at the generic level by Watson & Dallwitz (1985) and Watson, Dallwitz & Johnson (1986). Webster (1983) used the system in a revision of the genus *Digitaria* in Australia, and in a review of the grass tribe Paniceae in Australia in which 208 characters were recorded for 45 genera and 263 species (Webster 1987). The latter database will be used to generate a flora treatment for the Flora of Australia project (grass volumes are scheduled for 1988). These studies illustrate three important characteristics concerning the application of the DELTA computer programs to taxonomy. It is capable of storing and analyzing the data collected by taxonomists for revisions and floras without loss of information. The computer-produced descriptions are highly organized in terms of character sequence, terminology, and punctuation. In DELTA descriptions, commas are used where more than one character state applies to a character, semicolons are used between characters, and periods terminate a sequence of characters describing a primary feature. Parentheses separate comments from data available for key production. The result is standardization and unformity within and among descriptions. Finally, the taxonomist's concepts of key design and character reliability are reflected in the computer produced key. DELTA also ensures that information presented in the key agrees with descriptions.

The minor difficulties of adapting the taxonomist's working methods to this approach are outweighed by the obvious advantages of the system. These include the easy coding of descriptive data, accessible storage of data, efficient editing of data, and experimentation with various key designs. Other advantages are: (i) the capability of producing special purpose keys and taxa descriptions; (ii) the data are directly accessible for numerical analysis; (iii) the same data are directly accessible for online identification and information retrieval programs; (iv) output can be linked directly to automatic typesetting facilities; (v) the database is readily accessible for adding new taxa and data to the keys and descriptions. The DELTA method will be most useful in connection with any large group where these advantages justify the labor required to produce a comparative database.

METHODS

The taxonomic treatment presented here reflects the results of phenetic

and statistical analyses of 2,530 specimens from 245 populations of the section in North America (Webster 1981), where data were analyzed using the Statistical Analysis System (SAS) (Barr et al. 1976) and the Statistical Analysis System of Multivariate Statistical Programs (NT-SYS) package (Rohlf et al. 1971). Correlation and distance phenograms, principal components analysis, and multivariate analysis of variance were used to delineate population clusters. Basic statistical procedures such as character correlation coefficients, means, ranges, standard deviations, coefficients of variation, F-values, and nested analysis of variance were used to analyze character variation from within and among populations and between taxa. In the following species descriptions, comments made in the remarks section refer to data presented in Webster (1981). Representative voucher specimens are deposited at L, MO, NY, and US. A complete set of voucher specimens (*Webster 1790–2025*) is at TAES.

The descriptions of the genus and section were computer-produced from a character file designed to account for morphological variation in the Paniceae. Species descriptions were produced from a DELTA character list compiled specifically for the present study and include the quantitative morphological data from Webster (1981). The presence of parentheses within the descriptions serve the important function of distinguishing "comments" (i.e., information not available for key production) from the rest. For real numeric characters (i.e., spikelet length, leaf width, etc.) the means and full ranges are enclosed in parentheses. The expected or typical ranges precede the parentheses and were used by the programs in the key making processes. The expected range was arbitrarily calculated as the mean plus and minus two standard deviations. Full ranges cannot be used to produce useful keys for the taxa in a situation where overlaps occur for all taxonomically important real numeric characters. This problem is likely to arise in any group of closely related taxa, especially when a large sample size has been studied, and is certainly not peculiar to computer aided taxonomy.

The program KEY (Dallwitz 1978) allows for an interaction between the program and taxonomist, and there exists abundant scope for experimentation with key design. By the relative weighting of characters and taxa the taxonomist has ultimate control over the form of the key. If desired, the program can automatically select the best characters to satisfy the generation of mechanically efficient keys. The key presented here represents the most practical general purpose key of several generated. Anatomical and cytological characters were given a low weight of "1" and used as secondary characters; whereas, morphological characters were weighted relative to F-values from an analysis of variance by species

(Webster 1981). Of course, the taxonomist has the option of weighting the characters by any criteria he chooses including personal opinion. The key is based on data taken from North American specimens, however, there have been no difficulties in applying this treatment to specimens from other geographic regions.

TAXONOMY

DIGITARIA Haller, Hist. Stirp. Helv. 2:244. 1768, *nom. cons. prop.* *Panicum* sect. *Digitaria* Trin., Diss. Alt. 48, 76. 1826. *Panicum* series *Digitarieae* Benth., Fl. Austral. 7:464. 1878. *Paspalum* section *Digitaria* Hook. f., Fl. Br. Ind. 7:10. 1896. *Panicum* subgenus *Digitaria* Hackel, Oesterr. Bot. Z. 51:290. 1901. *Paspalum* subgenus *Digitaria* A. Camus, Not. Syst. 2:216. 1912. TYPE SPECIES: *Digitaria sanguinalis* (L.) Scop.

Valota Adans., Fam. Pl. 2:495. 1763. *Trichachne* Nees, Agrost. Bras. 85. 1829. *Panicum* section *Trichachne* Steudel, Syn. 1:38. 1853. *Panicum* series *Trichachne* Benth., Fl. Austr. 7:464. 1787. *Digitaria* subsection *Trichachne* Stapf, Fl. Trop. Afr. 9:424. 1919. *Digitaria* section *Trichachne* Henrard, Monogr. *Digitaria* 851, 866. 1950. TYPE SPECIES: *Digitaria insularis* (L.) Ekman.

Syntherisma Walter, Fl. Carol. 76. 1788. TYPE SPECIES: *D. sanguinalis* (L.) Scop.

Plants annual or perennial; erect or basally decumbent; 10 − 100 cm tall; sparingly branched or unbranched; with glabrous nodes (rarely hairy). Ligule a membrane (occasionally with fringed margins). Leaf blades flat to involute; hairy or glabrous; rounded or truncate at the base. Inflorescence a panicle. Main axis present or absent. Primary branches appressed or spreading; with secondary branches appressed or spreading; dorsiventral. Spikelet bearing branches terminating in a spikelet (bristles absent). Pedicels present; the apices truncate, discoid or cupuliform. Disarticulation at the base of the spikelet. Spikelets abaxial; not embedded in the rachis; plano-convex. First glume present or absent; not encircling the spikelet base; 0 − 1 nerved; muticous. Rachilla pronounced or not pronounced between the first and second glumes. Second glume 1 − 5 nerved; distinctly keeled or rounded on the back; membranous; muticous; 0.3 − 1.0 times lower lemma length. Lower floret neuter. Lower lemma membranous; muticous or mucronate. Palea of the lower floret absent or vestigial. Rachilla not well-developed between the florets. Upper lemma yellow to black; chartaceous to cartilaginous; smooth to muricate; margins flat and thinner than the body; glabrous; the apex muticous or mucronate. Palea of the upper floret smooth to muricate; enclosed.

DIGITARIA section DIGITARIA

Digitaria subsection *Sanguinales* Stapf, Gramineae. In Prain, Fl. Trop. Afr. 9:424. 1919. Section *Sanguinales* (Stapf) Henrard, Monogr. *Digitaria* 840. 1950.

Digitaria section *Horizontalis* Henrard, Monogr. *Digitaria* 586. 1950.
Digitaria section *Parviglumae* Henrard, Monogr. *Digitaria* 586. 1950.
Digitaria section *Biformes* Henrard, Monogr. *Digitaria* 815. 1950.

Annuals. Stolons absent. Flowering culms frequently decumbent and rooting at the lower nodes; 2 – 5 noded; 10 cm – 1 m tall; sparingly branched or unbranched; with glabrous nodes. Mid-culm sheaths not overlapping. Ligule margins erose. Blades with well-developed spicules on the margins. Inflorescence a panicle with spikelets appressed to racemose primary branches. Primary branches with spikelets on the basal portions. Pedicel apex truncate; without a corona of rigid hairs. Pedicel of the uppermost spikelet per grouplet not adnate on the lower portion to the primary branch. Spikelets paired; imbricate; ovate to lanceolate. Rachilla not developed between the first and second glume. Second glume 3-nerved. Lower lemma subequal or slightly longer than the upper lemma; hairy or glabrous; lacking a transverse line of hairs; indumentum villous or setaceous; villous hairs flattened, coiled and pointed; indumentum not overtopping the spikelet; indumentum absent between the mid-nerve and the first lateral nerve. Nerves of the lower lemma 5 – 7; not pronounced to the extent of producing slit-like interspaces; not anastomosing apically. Upper lemma yellow at maturity (frequently tinged purple); irregular striate at maturity; the apex acute to acuminate; the base not keeled. Flowering date, mostly June to November.

REMARKS: *Digitaria* section *Digitaria* consists of about ten species and is most closely related to sections *Heteranthae* Henrard and *Erianthae* Henrard. *Heteranthae* consists of two tropical Asian perennial species and may be the most primitive section within the genus. *Digitaria ctenantha* (F. Muell.) Hughes, a species native to tropical Australia, is morphologically intermediate between the sections *Digitaria* and *Heteranthae*. The *Erianthae* consists of about 25 perennial species native to Africa and are widely introduced as grasses for improved pastures. *Digitaria didactyla* Willd. is intermediate between sections *Erianthae* and *Digitaria*.

KEY TO DIGITARIA SECTION DIGITARIA IN NORTH AMERICA

1(0). Spikelets less than 2.8 mm long 2
Spikelets 2.8 mm long or more 5
2(1). Lower lemma with spicules on the lateral nerves; long cells 60 – 90 μm wide . . . . . *D. sanguinalis*
Lower lemma lacking spicules on the lateral nerves; long cells less than 50 μm wide 3
3(2). Second glume up to 0.35 times spikelet length; stomates averaging more than 35 μm wide . . . . . *D. setigera*
Second glume 0.4 – 0.7 times spikelet length; stomates averaging less than 35 μm wide 4

4(3). Blade of the uppermost leaf hairy on the adaxial surface; second glume 0.43 – 0.55 times spikelet length; sheath of the uppermost leaf usually with scattered long hairs . . . . . *D. horizontalis*
Blade of the uppermost leaf glabrous on the adaxial surface; second glume 0.57 – 0.7 times spikelet length; sheath of the uppermost leaf usually glabrous . . . . . *D. nuda*

5(1). Lower lemma with spicules on the lateral nerves; long cells 60 to 90 μm wide; prickles absent from the intercostal zones . . . . . *D. sanguinalis*
Lower lemma lacking spicules on the lateral nerves; long cells less than 60 μm wide; prickles rare in the intercostal zones 6

6(5). First glume absent or minute; second glume 0.15 – 0.35 times spikelet length; stomates averaging more than 35 μm wide . . . . . *D. setigera*
First glume present, more than 0.1 mm long; second glume more than 0.36 times spikelet length; stomates averaging less than 35 μm wide 7

7(6). Lower lemma of the sessile spikelet with equidistant nerves; lowermost inflorescence node glabrous or the hairs less than 0.4 mm long; apex of the first glume rounded to truncate . . . . . D. bicornis
Lower lemma of sessile spikelet with nerves crowded to the margins; lowermost inflorescence node with hairs greater than 0.4 mm long; apex of the first glume acute . . . . . *D. ciliaris*

DIGITARIA BICORNIS (Lam.) Roemer & Schultz, Syst. Veg. 2:470. 1817.

Paspalum bicorne Lam., Tabl. Encycl. 1:176. 1791. TYPE: *Sonnerat in Hb. Lamarck* (HOLOTYPE: P!).

Panicum adpressum Willd., Ges. Naturfr., Neue Schr. 4:193. 1803. TYPE: *Klein s.n.* (HOLOTYPE: B!; ISOTYPE: K!). *D. barbata* Willd., Enum. Hort. Berol. 1:91. 1809. *Panicum barbatum* (Willd.) Kunth, Revis. Gramin. 1:33. 1829. *Syntherisma barbata* (Willd.) Nash, Bull. Torrey Bot. Club 25:303. 1898.

Digitaria biformis Willd., Enum. Hort. Berol. 1:92. 1809. TYPE: *Bory de St. Vincent s.n.* (Hb. Willd. 1652, HOLOTYPE: B!). *Panicum biforme* (Willd.) Kunth, Revis. Gramin. 1:33. 1829.

Digitaria fimbriata Link, Hort. Berol. 1:226. 1827. TYPE: *Hb. Link 97* (HOLOTYPE: B!). *Panicum fimbriatum* (Link) Kunth, Revis. Gramin. 1:33. 1829. *Syntherisma fimbriata* (Link) Nash, Bull. Torrey Bot. Club 25:302. 1898.

Digitaria barbulata Desv., Opusc. Sci. Phys. Nat. 62. 1831. TYPE: *Hb. Desvaux s.n.* (HOLOTYPE: P!).

Panicum ciliare A. Rich., Tent. Fl. Abyss. 2:236. 1851. TYPE: *Schimper 1616* (HOLOTYPE: P!; ISOTYPES: K, L).

Digitaria chrysoblephara Figari & De Notaris, Ac. Rle. Sc. Torino Class. Fis. & Mat. II, 14:364. 1852. TYPE: *Figari s.n.* (HOLOTYPE: FL). *D. adscendens* Henrard ssp. *chrysoblephara* (Figari & De Notaris) Henrard, Monogr. Digitaria 125. 1950. *D. ciliaris* Koeler ssp. *chrysoblephara* (Gigari & De Notaris) S.T. Blake, Proc. Roy. Soc. Qld. 81:12. 1969. *D. ciliaris* var. *chrysoblephara* (Figari & De Notaris) R.R. Steward, Kew Bull. 29(2):444. 1974. *D. biformis* var. *chrysoblepharis* (Figari & De Notaris) Beetle, Phytologia 49:38. 1981.

Panicum sanguinale L. var. *barcaldinese* Domin., Biblioth. Bot. 85:295. 1915. TYPE: *Domin 1016* (HOLOTYPE: PR!).

Digitaria queenslandica Henrard, Monogr. *Digitaria* 612. 1950. TYPE: *Simmons s.n.* (HOLOTYPE: W!; ISOTYPE: NSW!).

Digitaria diversiflora Swallen, Rhodora 65:356. 1963. TYPE: *Hitchcock 9636* (HOLOTYPE: US!).

Sheath of the uppermost leaf 77 – 181 mm long (129, 62 – 230); usually with scattered long hairs. Ligule 0.9 – 2.7 mm long (1.8, 0.6 – 3.5). Blade of the uppermost leaf 18 – 130 mm long (64, 18 – 338); 2 – 7.4 mm wide (4.55, 2 – 10); glabrous on the adaxial surface; usually with a few setaceous hairs at the leaf blade base. The lowermost inflorescence node glabrous or the hairs shorter than 0.4 mm. Inflorescence main axis 0 – 22 mm long (4.0, 0 – 50). Lowermost primary branch of the inflorescence 74 – 166 mm long (120, 63 – 224); 0.7 – 1.2 mm wide (0.93, 0.6 – 1.3); lacking seta on the branch body (rarely present). Primary branches occurring singly (not paired nor in whorls), 0 – 1(0 – 3). Pedicel 1.3 – 2.9 mm long (2.1, 1.0 – 4.2). Number of spikelets per 1.4 cm of primary branch, 5 – 12 (8, 5 – 13). Spikelets 2.8 – 3.6 mm long (3.2, 2.6 – 3.7); 0.8 – 1 mm wide (0.9, 0.7 – 1.1). First glume 0.12 – 0.37 mm long (0.25, 0 – 0.8); cleft to rounded (rarely acute). Second glume 1.9 – 2.7 mm long (2.3, 1.7 – 2.8); 0.65 – 0.91 times spikelet length (0.77, 0.65 – 0.93). Distance from the midnerve to the first lateral nerve on the lower lemma of the sessile spikelet, 0.15 – 0.23 mm (0.19, 0.13 – 0.30). Distance from the midnerve to the first lateral nerve on the lower lemma of the pedicelled spikelet, 0.17 – 0.28 mm (0.22, 0.17 – 0.30). Lower lemma lacking spicules on the lateral nerves; with setaceous hairs on the marginal interspaces, or lacking setaceous hairs on the marginal interspaces.

ABAXIAL LEAF EPIDERMIS. Long cells in 11 – 25 (18, 9 – 30) rows between adjacent costal zones; 73 – 113 (93, 42 – 150) μm long; 21 – 32 (mean 27) μm wide. Prickles common on the intercostal zones. Stomates 32 μm long (average); 29 μm wide (average); 1 – 3 rows between adjacent costal zones. Average length of bicellular microhairs 76 μm. Average length of silica cells 27 μm. Average pollen diameter 34 μm. Chromosome number $2n = 72$.

DISTRIBUTION: Tropics and subtropics of the world. In North America this species occurs on the sandy coastal plain of the southeastern United States from North Carolina to Texas. It is common throughout the Caribbean and coastal areas of Mexico.

REMARKS: This species is most similar to *D. ciliaris*, and in warm temperate to tropical areas populations of these species frequently grow intermingled. Typically, *Digitaria bicornis* is yellow-green and either lacks an inflorescence main axis or has primary branches positioned in whorls,

whereas, *D. ciliaris* is usually dark green with some of the primary branches solitary. Statistical analysis showed these species to differ significantly in 17 of the 23 measured morphological characters. *Digitaria bicornis* has a significantly shorter first glume, longer second glume, smaller distance between the nerves of the lower lemma, and a shorter inflorescence axis.

Previous taxonomic treatments of *Digitaria* used the presence or absence of setaceous hairs on the lower lemma for describing and identifying certain species. *Digitaria bicornis*, as presented in this study, is variable for the presence of this hair type. Phenetic and statistical comparison among populations with setaceous hairs and populations without setaceous hairs showed that there were no significant differences. Populations with setaceous hairs on the lower lemma usually occur in tropical areas. Typically, the lower lemma of the sessile spikelet is glabrous or nearly so, and this lemma on the pedicellate spikelet is densely hairy. However, this relationship is variable and of limited taxonomic value.

DIGITARIA CILIARIS (Retz.) Koeler, Descr. Gram. 27. 1802. *Panicum ciliare* Retz., Observ. Bot. 4:16. 1786. TYPE: *Wennenberg s.n.* in Hb. Retzius (LECTOTYPE: LD!). *D. sanguinalis* Scop. var. *ciliaris* (Retz.) Parl., Fl. Ital. 1:126. 1848. *D. sanguinalis* (L.) Scop. ssp. *ciliaris* (Retz.) Arcang., Fl. Ital. 762. 1882.

Panicum adscendens Kunth, Nov. Gen 1:80. 1815. TYPE: *Humbolt s.n.* (LECTOTYPE: P; ISOTYPES: B!, BM!). *D. adscendens* (Kunth) Henrard, Blumea 1:92. 1934.

Digitaria marginata Link, Enum. Berol. 1:102. 1821. TYPE: *Hb. Link 97* (HOLOTYPE: B). *Syntherisma marginata* (Link) Nash, N. Amer. Fl. 17:154. 1912. *D. sanguinalis* var. *marginata* (Link) Fern., Rhodora 22:103. 1920.

Digitaria abortiva Reeder, J. Arnold Arbor. 29:291. 1948. TYPE: *Carr 11108* (HOLOTYPE: US!; ISOTYPES: BM, CANB!, L).

Sheath of the uppermost leaf 51 – 171 mm long (111, 48 – 178); usually with scattered long hairs. Ligule 1.3 – 3.1 mm long (2.2, 1.0 – 4.0). Blade of the uppermost leaf 15 – 144 mm long (74, 15 – 189); 3 – 9 mm wide (5.9, 3 – 9); glabrous on the adaxial surface; usually with a few setaceous hairs at the leaf blade base. The lowermost inflorescence node hairy, the hairs longer than 0.4 mm. Inflorescence main axis 2.5 – 50 mm long (26.5, 0 – 93). Lowermost primary branch of the inflorescence 61 – 169 mm long (115, 41 – 241); 0.7 – 1.2 mm wide (0.92, 0.7 – 2.0); lacking seta on the branch body. Primary branches occurring singly (not paired nor in whorls), 0 – 6 (2, 0 – 7). Pedicel 1.2 – 3 mm long (2.1, 1.0 – 3.7). Number of spikelets per 1.4 cm of primary branch, 6 – 14 (10, 6 – 24). Spikelets 2.8 – 3.6 mm long (3.2, 2.7 – 4.1); 0.78 – 1 mm wide (0.89, 0.6 – 1.1). First glume 0.24 – 0.52 mm long (0.38, 0.2 – 0.8); acute. Second glume 1.5 – 2.2 mm long (1.85, 1.2 – 2.7); 0.6 – 0.85 times spikelet length (mean 0.7). Distance from

the midnerve to the first lateral nerve on the lower lemma of the sessile spikelet, 0.24 − 0.34 mm (0.28, 0.17 − 0.37). Distance from the midnerve to the first lateral nerve on the lower lemma of the pedicelled spikelet, 0.24 − 0.36 mm (0.3, 0.2 − 0.4). Lower lemma lacking spicules on the lateral nerves; with setaceous hairs on the marginal interspaces, or lacking setaceous hairs on the marginal interspaces.

Abaxial leaf epidermis. Long cells in 3 − 19 (mean 7) rows between adjacent costal zones; 45 − 210 (mean 120) μm long; 27 to 54 (mean 36) μm wide. Prickles common on the intercostal zones. Stomates 37 μm long (average); 30 μm wide (average); 2 − 6 rows between adjacent costal zones (mean 3). Average length of bicellular microhairs 82 μm. Average length of silica cells 22 μm. Average pollen diameter 33 μm. Chromosome number $2n = 54$.

DISTRIBUTION: Temperate and tropical regions of the world. In North America it occurs throughout the Caribbean, Mexico, and most of the United States. It does not normally extend into Canada.

REMARKS: The morphology of *D. ciliaris* links the members of the section. It integrades with *D. sanguinalis* in temperate regions, *D. bicornis* in tropical regions, *D. nuda* in Africa, and with *D. radicosa* (Presl.) Miq. and *D. setigera* in India and Asia. *Digitaria horizontalis* and *D. velutina* are linked to *D. ciliaris* by *D. nuda*. *Digitaria ciliaris* is variable for the presence or absence of setaceous hairs on the lower lemma. There are no significant phenetic or statistical differences between the two forms. A comparison between the setaceous forms of *D. bicornis* and *D. ciliaris* showed many significant differences.

DIGITARIA HORIZONTALIS Willd., Enum. Hort. Berol 1:92. 1809. TYPE: *Hb. Willd. 1654* (HOLOTYPE: B, photograph!). *Panicum horizontale* (Willd.) G. Meyer, Prim. Fl. Esseq. 54. 1818. *D. sanguinalis* var. *horizontalis* (Willd.) Rendle, Cat. Afr. Pl. Welw. 2:163. 1899. *Panicum sanguinale* ssp. *horizontale* (Willd.) Hackel, Ergeb. Bot. Exped. Akad. Wiss. Sudbras. 8. 1906.

Digitaria setosa Desv. ex Ham., Prodr. Pl. Occ. 6 (1825). TYPE: *Hb. Desvaux* (HOLOTYPE: P). *Syntherisma setosum* (Desv. ex Ham.) Nash, Bull. Torrey Bot. Club 25:300. 1898.

Sheath of the uppermost leaf 67 − 163 mm long (115, 55 − 163); usually with scattered long hairs. Ligule 0.5 − 1.5 mm long (1.02, 0.5 − 1.7). Blade of the uppermost leaf 24 − 108 mm long (60.9, 24 − 122); 3 − 8.9 mm wide (5.5, 3 − 12); hairy on the adaxial surface; usually with a few setaceous hairs at the leaf blade base. The lowermost inflorescence node hairy, the hairs longer than 0.4 mm. Inflorescence main axis 5 − 57 mm long (31.4, 0 − 60). Lowermost primary branch of the inflorescence 62 − 144 mm long (102.1, 62 − 153); 0.4 − 0.65 mm wide (0.52,

0.4 – 0.7); with seta present on the branch body. Primary branches occurring singly (not paired nor in whorls), 0 – 5 (2, 0 – 6). Pedicel 0.9 – 2.4 mm long (1.6, 0.9 – 3.0). Number of spikelets per 1.4 cm of primary branch, 8 – 15 (11, 6 – 16). Spikelets 2 – 2.6 mm long (2.3, 1.9 – 2.7); 0.47 – 0.61 mm wide (0.53, 0.47 – 0.67). First glume 0.08 – 0.24 mm long (0.16, 0 – 0.30); acute. Second glume 0.8 – 1.5 mm long (1.1, 0.8 – 2.1); 0.43 – 0.55 times spikelet length (mean 0.50). Distance from the midnerve to the first lateral nerve on the lower lemma of the sessile spikelet, 0.1 – 0.17 mm (0.13, 0.10 – 0.17). Distance from the midnerve to the first lateral nerve on the lower lemma of the pedicelled spikelet, 0.1 – 0.17 mm (0.13, 0.10 – 0.17). Lower lemma lacking spicules on the lateral nerves; lacking setaceous hairs on the marginal interspaces.

ABAXIAL LEAF EPIDERMIS. Long cells in 15 – 30 (mean 18) rows between adjacent costal zones; 30 – 120 (mean 67) μm long; 20 – 40 (mean 27) μm wide. Prickles absent from the intercostal zones. Stomates 32 μm long (average); 29 μm wide (average); 2 – 4 rows between adjacent costal zones. Average length of bicellular microhairs 64 μm. Average length of silica cells 21 μm. Average pollen diameter 37 μm. Chromosome number $2n = 36$.

DISTRIBUTION: Tropics of the world. In North America this species occurs in southern Florida, throughout the Caribbean, coastal areas of Mexico, and the southern part of Baja California.

REMARKS: *Digitaria horizontalis* was shown to be most similar to *D. nuda*. These species can be distinguished from other North American members of the section by the presence of bulbose-based hairs on the primary branches. These hairs are commonly located on the body of the primary branch at the base of a spikelet pair. Rarely specimens of *D. sanguinalis* and *D. setigera* possess these hairs. *Digitaria velutina* (Forssk.) P. Beauv., native to Africa, is also similar to *D. horizontalis*, but has spikelets less than 2.1 mm long.

DIGITARIA NUDA Schum., Beskr. Guin. Pl. 65. 1827. TYPE: *Thonner* 367 (HOLOTYPE: C!).

Milium digitatum Sw., Prodr. Veg. Ind. Occ. 24. 1788. TYPE: *Swartz s.n.* (HOLOTYPE: S). *Agrostis digitata* (Sw.) Poir, Encycl. Sup. 1:258. 1810. *Axonopus digitatus* (Sw.) P. Beauv., Essai Agrost. 12:154. 1812. *Paspalum digitatum* (Sw.) Kunth, Revis. Gramin. 1:24. 1829. *Syntherisma digitatum* (Sw.) Hitchc., Contr. U.S. Natl. Herb. 12:142. 1908.

Sheath of the uppermost leaf 37 – 150 mm long (91.7, 37 – 155); usually glabrous (or occasionally with a few scattered hairs). Ligule 0.8 – 2 mm long (1.34, 0.8 – 2.5). Blade of the uppermost leaf 24 – 129 mm long (65.4, 24 – 163); 4 – 10.2 mm wide (5.7, 4 – 13); glabrous on the adaxial

surface; usually with a few setaceous hairs at the leaf blade base. The lowermost inflorescence node hairy, the hairs longer than 0.4 mm. Inflorescence main axis 0 – 52 mm long (17.2, 0 – 65). Lowermost primary branch of the inflorescence 45 – 148 mm long (91.6, 44 – 154); 0.4 – 0.8 mm wide (0.64, 0.4 – 0.8); with seta present on the branch body, or lacking seta on the branch body. Primary branches occurring singly (not paired nor in whorls), 0 – 4 (1, 0 – 5). Pedicel 0.5 – 2.5 mm long (1.5, 0.5 – 3.0). Number of spikelets per 1.4 cm of primary branch, 7 – 20 (14, 7 – 20). Spikelets 2.1 – 2.7 mm long (2.4, 2.1 – 2.8); 0.58 – 0.78 mm wide (0.7, 0.53 – 0.80). First glume 0 – 0.17 mm long (0.07, 0 – 0.17); rounded to acute (when present). Second glume 1 – 2.1 mm long (1.53, 1.0 – 2.2); 0.57 – 0.7 times spikelet length (mean 0.63). Distance from the midnerve to the first lateral nerve on the lower lemma of the sessile spikelet, 0.13 – 0.2 mm (0.16, 0.13 – 0.20). Distance from the midnerve to the first lateral nerve on the lower lemma of the pedicelled spikelet, 0.14 – 0.22 mm (0.18, 0.13 – 0.23). Lower lemma lacking spicules on the lateral nerves; lacking setaceous hairs on the marginal interspaces.

ABAXIAL LEAF EPIDERMIS. Long cells in 8 – 20 rows between adjacent costal zones; 50 – 100 μm long; 25 – 40 μm wide. Prickles common on the intercostal zones, or absent from the intercostal zones. Stomates 30 μm long (average); 27 μm wide (average); 2 – 4 rows between adjacent costal zones. Average length of bicellular microhairs 74 μm. Average pollen diameter 37 μm. Chromosome number $2n = 36$.

DISTRIBUTION: Tropics of Africa, Asia and the Americas. In North America it occurs in Florida, the Caribbean, and in tropical and subtropical regions of Mexico and Central America.

REMARKS: A phenetic analysis comparing 60 specimens of *D. horizontalis* with 30 specimens of *D. nuda* did not clearly separate two clusters. A statistical comparison showed *D. horizontalis* has a significantly smaller spikelet width. In addition, it has hairy leaves, whereas, the leaves of *D. nuda* are glabrous. It is concluded that these species are closely related, but should be recognized as distinct.

DIGITARIA SANGUINALIS (L.) Scop., Fl. Carn. ed. 2, 1:52. 1772. *Panicum sanguinale* L., Sp. Pl. 57. 1753. TYPE: *Van Royen* (LECTOTYPE: L). *Dactylon sanguinale* (L.) Villars, Hist. Pl. Dauph. 2:69. 1787. *Syntherisma sanguinalis* (L.) Dulac, Fl. Haut. Pyr. 77. 1876.

Sheath of the uppermost leaf 58 – 166 mm long (112, 36 – 168); usually with scattered long hairs. Ligule 0.6 – 1.85 mm long (1.23, 0.5 – 2.6). Blade of the uppermost leaf 14 – 164 mm long (84, 14 – 210); 2.8 – 11.6 mm wide (7.2, 2 – 13); hairy on the adaxial surface; usually with a few

setaceous hairs at the leaf blade base. The lowermost inflorescence node hairy, the hairs longer than 0.4 mm. Inflorescence main axis 0 – 45 mm long (17.3, 0 – 87). Lowermost primary branch of the inflorescence 57 – 173 mm long (115.4, 34 – 194); 0.76 – 1.44 mm wide (1.1, 0.7 – 1.5); lacking seta on the branch body (only rarely present). Primary branches occurring singly (not paired nor in whorls), 0 – 3 (1, 0 – 7). Pedicel 1.1 – 2.7 mm long (1.95, 1.0 – 3.1). Number of spikelets per 1.4 cm of primary branch, 6 – 14 (10, 5 – 17). Spikelets 2.5 – 3.3 mm long (2.9, 1.7 – 3.4); 0.75 – 0.99 mm wide (0.87, 0.73 – 1.12). First glume 0.13 – 0.45 mm long (0.29, 0.05 – 0.87); acute. Second glume 1 – 1.8 mm long (1.44, 0.9 – 2.0); 0.4 – 0.75 times spikelet length (mean 0.55). Distance from the midnerve to the first lateral nerve on the lower lemma of the sessile spikelet, 0.19 – 0.31 mm (0.25, 0.17 – 0.33). Distance from the midnerve to the first lateral nerve on the lower lemma of the pedicelled spikelet, 0.21 – 0.33 mm (0.27, 0.20 – 0.37). Lower lemma with spicules on the lateral nerves; lacking setaceous hairs on the marginal interspaces.

Abaxial leaf epidermis. Long cells in 6 – 20 (mean 8) rows between adjacent costal zones; 33 – 114 (mean 78) μm long; 60 – 90 (mean 69) μm wide. Prickles absent from the intercostal zones. Stomates 32 μm long (average); 27 μm wide (average); 2 – 6 (mean 4) rows between adjacent costal zones. Average length of microhairs 69 μm. Average length of silica cells 21 μm. Average pollen diameter 29 μm. Chromosome number $2n = 36$.

Distribution: Temperate regions of the world. In North America this species occurs on loamy soils in disturbed open areas. It is common in the north central United States, extending northward into southern Canada, westward to California, and southward into northern parts of Alabama, Louisiana, Texas, and Mexico.

Remarks: In areas of sympatry, populations of *D. ciliaris* and *D. sanguinalis* frequently grow intermingled, and they are difficult to distinguish. A phenetic analysis of 160 populations (1600 specimens) clearly separated the species, and a statistical comparison showed significant differences in 13 morphological characters. *Digitaria sanguinalis* has papillose-based hairs on the leaf blades, spicules on the lateral nerves of the lower lemma, a relatively shorter second glume, and a longer ligule. Specimens of *D. ciliaris* rarely have hairs on the leaf blades, spicules on the lateral nerves of the lower lemma, or a relatively short second glume. They never possess these characters in combination.

Digitaria setigera Roemer & Schultz, Syst. Veg. 2:474. 1817. Type: *Heyne s.n.* (holotype: K!).

Panicum pruriens Fisher ex Trin., Diss. Alt. 77. 1826. TYPE: *Chamisso s.n.* in Hb. Trinius (HOLOTYPE: LE; ISOTYPE: K!). *Digitaria pruriens* (Fisher ex Trin.) Buse in Mig., Pl. Jungh. 379. 1854.

Panicum microbachne C. Presl, Reliq. Haenk. 1:298. 1830. TYPE: *Haenke s.n.* (HOLOTYPE: PR!; ISOTYPE: W). *Digitaria microbachne* (C. Presl) Henrard, Meded. Rijksherb Leiden 61:13. 1930. *D. pruriens* (Fisher ex Trin.) Buse var. *microbachne* (C. Presl) Fosb., Phytologia 5:289. 1955.

Sheath of the uppermost leaf 80.3 – 169 mm long (127.1, 57 – 169); usually with scattered long hairs. Ligule 1.7 – 3.3 mm long (2.5, 1.4 – 3.5). Blade of the uppermost leaf 60 – 157 mm long (102.4, 60 – 180); 4 – 11.4 mm wide (7.4, 4 – 13); hairy on the adaxial surface, or glabrous on the adaxial surface; usually with a few setaceous hairs at the leaf blade base. The lowermost inflorescence node hairy, the hairs longer than 0.4 mm. Inflorescence main axis 0 – 63 mm long (31.1, 0 – 75). Lowermost primary branch of the inflorescence 77 – 161 mm long (119, 60 – 164); 0.52 – 0.96 mm wide (0.74, 0.5 – 1.0); lacking seta on the branch body (rarely present). Primary branches occurring singly (not paired nor in whorls), 0 – 5 (2, 0 – 7). Pedicel 1 – 2.4 mm long (1.7, 0.9 – 2.7). Number of spikelets per 1.4 cm of primary branch, 7 – 14 (10, 7 – 14). Spikelets 2.6 – 3.2 mm long (2.9, 2.5 – 3.2); 0.6 – 0.78 mm wide (0.72, 0.6 – 0.8). First glume 0 – 0.06 mm long (0.01, 0.0 – 0.1). Second glume 0.3 – 1.1 mm long (0.6, 0.3 – 1.1); 0.15 – 0.35 times spikelet length (mean 0.27). Distance from the midnerve to the first lateral nerve on the lower lemma of the sessile spikelet, 0.17 – 0.23 mm (0.21, 0.17 – 0.23). Distance from the midnerve to the first lateral nerve on the lower lemma of the pedicelled spikelet, 0.18 – 0.26 mm (0.22, 0.17 – 0.27). Lower lemma lacking spicules on the lateral nerves; with setaceous hairs on the marginal interspaces, or lacking setaceous hairs on the marginal interspaces.

ABAXIAL LEAF EPIDERMIS. Long cells in 5 – 10 (mean 8) rows between adjacent costal zones; 45 – 135 (mean 95) μm long; 24 – 36 μm wide. Prickles common on the intercostal zones. Stomates 30 μm long (average); 40 μm wide (average); 1 – 2 rows between adjacent costal zones. Average length of microhairs 82 μm. Average length of silica cells 24 μm. Average pollen diameter 40 μm. Chromosome number $2n = 72$.

DISTRIBUTION: Tropical Asia, probably introduced into North America. This species occurs in southern Florida, throughout the Caribbean, southern Mexico and Central America.

REMARKS: In many of the sections of *Digitaria*, taxa occur with a distinct reduction in the relative sizes of the glumes. In the section *Digitaria*, this trend is most pronounced in *D. setigera*, where first glume is absent and the second glume is very short relative to spikelet length. When

applied in combination, these characters readily distinguish this species. A statistical analysis showed that specimens with hairy leaves were otherwise identical to specimens with glabrous leaves. That is, if leaf pubescence were disregarded, then it would be impossible to differentiate between specimens traditionally named *D. microbachne* and *D. setigera*. It is concluded that *D. microbachne* should be treated as a synonym of *D. setigera*. Webster & Hatch (1981) first reported the presence of *D. setigera* and *D. nuda* in the New World.

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COUTAPORTLA PAILENSIS (RUBIACEAE), A NEW SPECIES FROM COAHUILA, MÉXICO

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ABSTRACT

Coutaportla pailensis is described from the Sierra de la Paila, southern Coahuila, México. Its closest relative appears to be *C. ghiesbreghtiana* from central México from which it differs in a number of salient features.

A new species of *Coutaportla* has recently been discovered in the Sierra de la Paila of southern Coahuila. This is the third known species of this New World genus. The other two species include *C. ghiesbreghtiana* (Baillon) Urban of central México and the recently described *C. guatemalensis* Lorence (Lorence 1986) of southern México and Guatemala. The Sierra de la Paila is the northernmost point of distribution not only for the genus but for the tribe Condamineeae.

COUTAPORTLA **pailensis** Villarreal, sp. nov. Fig. 1.

Frutex 10 – 40 cm altus. Laminae foliorum ellipticae vel orbiculares, 4 – 12 cm longae, 3 – 9 mm latae, coriaceae, minute papillosae. Inflorescentia terminalis simplex. Flores roseoli infundibuliformes, 2 – 3.8 cm longi, distaliter 1.5 – 2.8 mm diametro. Capsula oblonga 8 – 16 mm longa, 4 – 5 mm lata, placenta centralis, semina 4 – 10 in quoque loculo, elliptica, 3 – 4 mm longa, 2 – 2.5 mm lata.

Rounded, compact shrublets 10 – 40 cm high. Stems minutely pubescent, terete, nodes prominent, internodes 1 – 8 mm long. Stipules persistent, interpetiolar, broadly deltoid, 0.6 – 0.8 mm long, 1.2 – 1.5 mm wide, colleters 1 – 4 on each margin and one apical. Leaves opposite; petioles short, 0.5 – 2 mm long, flattened, distally winged; blades elliptic to orbicular, 4 – 12 mm long, 3 – 9 mm wide, coriaceous, minutely papillose, green-yellow, apices rounded, mucronulate, base cuneate-decurrent, margin entire. Inflorescence terminal, simple, each flower subtended by four lanceolate bracteoles 1 – 3 mm long. Flowers tetramerous (rarely pentamerous), pedicels 2 – 4 mm long; hypanthium 3 – 5 mm long; calyx 4(– 5)-lobed, foliaceous, narrowly triangular, carinate, 3 – 6 mm long, erect, with red-tipped glands along each margin; corolla pink, funnelform, 2 – 3.8 cm long, 1.5 – 2.8 mm in diameter distally, glabrous, tube 1.6 – 3.0 cm long, lobes triangular-ovate, 8 – 12 mm long; stamens 4 (or

SIDA 12(1): 223 – 225. 1987.

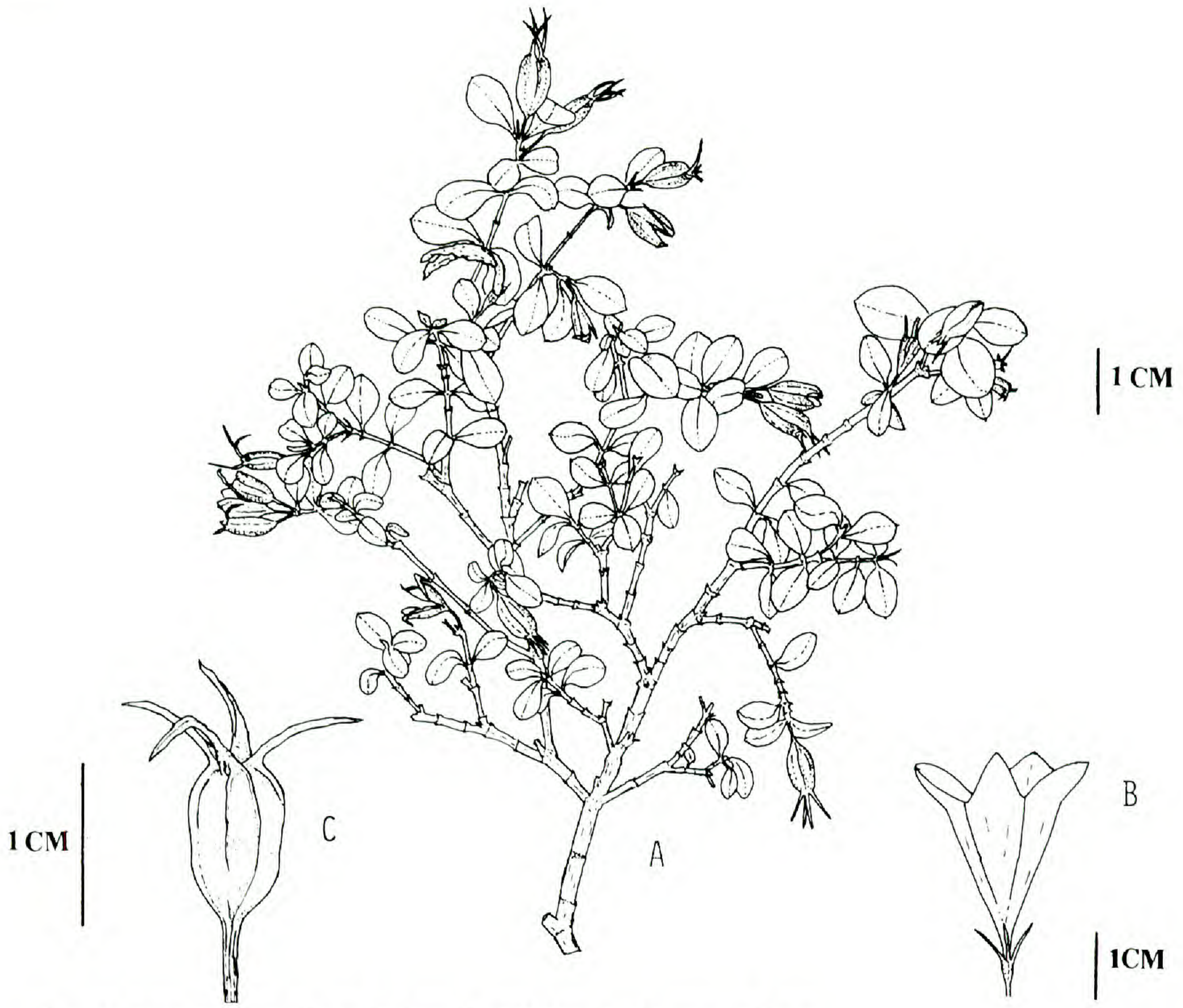

Fig. 1. *Coutaportla pailensis* Villarreal. a) Habit, b) Flower, c) Fruit.

5), included, 2 larger with anthers 6 mm long and filaments 1 cm long, 0.2 mm wide, the two (or three) shorter anthers 5 mm long, filaments 4 mm long, 0.4 mm wide, anthers linear, basifixed; style filiform, glabrous, 1 – 2.5 cm long; stigma bilobed. Capsule oblong, 8 – 10 mm long, 4 – 5 mm wide, bilocular, compressed, brown, glabrate, dehiscence longitudinal-septicidal, calyx-lobes persistent; placenta central, upper and lower seeds 2 – 5 in each locule; seeds vertical, elliptic, 3 – 4 mm long, 2 – 2.5 mm wide, brown, thickened at the margins, testa reticulate.

TYPE: MÉXICO. COAHUILA, Mpio. Ramos Arizpe, Sierra de la Paila, Cañón de Loma Prieta, al NW de Hipólito (25°51′N lat, 101°30′W long), 1800 m, paredes rocosas creciendo con *Hemichaena*, *Poliomintha*, *Emorya*, y *Randia*, *6 Agosto 1986, Jose A. Villareal et al. 3305* (HOLOTYPE: MEXU; ISOTYPES: ANSM, ENCB, TEX).

Additional specimen examined: topotype, 23 Oct 1985, *José A. Villareal et al. 3063* (ANSM).

Coutaportla pailensis is a very distinct species. It can be distinguished by

its compact, shrubby habit, small leaves, a simple inflorescence, besides its rather oblong capsule, elliptic seeds, and higher variability in number of seeds (4 – 10) per locule. It seems that the more closely related species is *C. ghiesbreghtiana*, with which it shares the following features: interpetiolar stipules, terminal position of the inflorescence, red glandular calyx lobe margins (these are not very conspicuous in *C. pailensis*).

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EUSTACHYS CARIBAEA (POACEAE), A SPECIES NEW TO THE UNITED STATES AND A KEY TO *EUSTACHYS* IN THE UNITED STATES

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ABSTRACT

Eustachys caribaea (Sprengel) Herter was recently collected from Calcasieu Parish, Louisiana and represents the first report of this South American taxon in the United States. A previous report of this species under the name *Chloris capensis* (Houtt.) Thell. has proved to be erroneous. The method of introduction is unknown but, it appears to have been unintentional. Two other adventive and four native species of *Eustachys* are now known in the United States.

Prior to this report, four native and two adventive species of *Eustachys* were known to occur in the United States for this primarily subtropical and tropical New World genus. *Eustachys neglecta* (Nash) Nash is endemic to Florida; *E. floridana* Chapm. occurs in Alabama, Florida and Georgia; *E. glauca* Chapm. ranges from Florida to North Carolina; and *E. petraea* (Sw.) Desv. is distributed from New Jersey to Florida and Texas. Among the adventive species, *E. retusa* (Lagasca) Kunth (*Chloris argentina* (Hackel) Lillo & Parodi) has been recorded in Georgia, New York, South Carolina, and Texas and *E. distichophylla* (Lagasca) Nees is a probable escape from cultivation in southern California, Florida, and Texas (Nash 1898; Chase 1951; Gleason 1952; Radford et al. 1968; Anderson 1975; Allen 1980).

This paper reports the occurrence of *E. caribaea* (Sprengel) Herter which represents a third species of this genus introduced to the U.S. Specimens of this taxon were first collected by Paul McKenzie on 26 May 1985 from a

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population of about 200 plants in Calcasieu Parish, along Interstate 10 near Sulphur, Louisiana. The plants were growing in sandy loam soil within one meter of the highway surface associated with *Cenchrus incertus* M. Curtis, *Paspalum notatum* Fluegge, *P. urvellei* Steudel, *P. dilatatum* Poiret and *Cynodon dactylon* (L.) Pers. Chase (1951) reported *E. caribaea* from Florida under the misapplied name *Chloris capensis* (Houtt.) Thell. However, this and subsequent records from the U.S. proved to be *E. distichophylla* (Dr. D. Hall, pers. comm., Univ. Fla., Gainesville). Hall (pers. comm.) reports Brazilian material of *E. caribaea* was grown at the Plant Introduction Garden, Gainesville, Florida (Lilian E. Arnold, plant introduction number 203625), but it is not known to have escaped.

Eustachys caribaea is native to Bolivia, Brazil, Argentina, Paraguay and Uruguay (Cabrera 1970; Smith et al. 1981). Its method of introduction into the U.S. is not known. Cabrera (1970) and Smith et al. (1981) note that *E. caribaea* has little or moderate forage value. Records of the Iberia (Jeanerette, LA) and Crowley (Crowley, LA) Research Stations which are near the discovery area indicate this species has not been grown experimentally in the area (H. Viator and J. Griffin, pers. comm., respectively). It is unlikely that the grass entered the U.S. from South America via a seed source used to sow the highway median and shoulders following construction. Mr. L. Sellers (pers. comm., Kaufman Seed Co., Ashdown, Arkansas, a distributor of grass seed in the South) indicates that most commercial grass seed for this purpose is grown in east Texas and Florida. Perhaps the grass entered through the Port of Lake Charles and was subsequently spread by vehicles transporting cargo from the port along Interstate Highway 10.

Some authors have given *Eustachys* infrageneric status in *Chloris* (e.g. Hitchcock 1951). Nash (1898) supported treating *Eustachys* as a separate genus as have more recent workers including Sanchez (1971) and Anderson (1974, 1975). Differences in generic concepts notwithstanding, the correct specific epithet for *Eustachys caribaea* is somewhat controversial. Rosengurtt and Izaguirre (1968) use *Chloris bahiensis* Steud. and regard *Chloris caribaea* as nomen dubium. A fragment of the type in US originating from the Berlin Herbarium, annotated as "*Chloris caribaea* Spr. Hb. Krug et Urban," they maintain, cannot positively be determined as the same as *Chloris bahiensis*. On the other hand, Hitchcock (in adnot.) examined the type in the Krug and Urban Herbarium and concluded that it and *C. bahiensis* are the same (Chase and Niles 1962). Anderson (1974) and Smith et al. (1981) evidently accept Hitchcock's assessment of the situation.

The name *Chloris capensis* (Houtt.) Thell. has also been used for *E. caribaea*. Anderson (1974) states this name is based on *Andropogon capense*

Houtt. which in turn is based on *A. muticum* L.; material of the latter in the Linnaean Herbarium is unidentifiable and, therefore, would be regarded as nomen dubium. Several combinations have been the result of Thellung's (1912) misinterpretation (see "Excluded Names" following the taxonomic treatment).

Superficially, *E. caribaea* resembles *E. petraea* in habit but its spikelets are noticeably lighter in color, the cilia along the keel and margins are longer, and its sterile florets are more truncate at the apex. Because morphological details of this species are not readily available in the literature, an illustration (Fig. 1) and description are provided. A key to the species of *Eustachys* known in the U.S. is included to facilitate identification.

KEY TO EUSTACHYS IN THE UNITED STATES

a. Lateral nerves of the fertile lemma glabrous ..... *E. glauca*
a. Lateral nerves of the fertile lemma pubescent ..... b
  b. Keel of fertile lemma glabrous c
    c. Spikelets shorter than 2.1 mm; sterile floret widely cuneate, truncate ..... *E. retusa*
    c. Spikelets 2.4 mm or long; sterile floret oblanceolate, acute ... *E. distichophylla*
  b. Keel of fertile lemma ciliate ..... d
    d. Spikelets shorter than 2.5 mm ..... e
      e. Spikelets dark brown to black; cilia on lemma of lower floret shorter than 0.5 mm ..... *E. petraea*
      e. Spikelets tawny to reddish brown; cilia on lemma of lower floret longer than 0.5 mm ..... *E. caribaea*
    d. Spikelets longer than 2.5 mm ..... f
      f. Spikes usually 1 – 3; spikelets 3 mm or longer; fertile lemma awn 0.6 mm or shorter ..... *E. floridana*
      f. Spikes usually 4 – 9; spikelets 3 mm or shorter; fertile lemma awn 0.6 mm or shorter ..... *E. neglecta*

EUSTACHYS CARIBAEA (Sprengel) Herter, Revista Sudamer. Bot. 6:147. 1940. *Chloris caribaea* Sprengel, Syst. Veg. 1:295. 1825. TYPE: reportedly from Guadaloupe, but the locality is probably in error (Chase and Niles 1962), [B, destroyed; as fragments: US, BAA (Rosengurtt and Izaguirre 1968)].

Eustachys distichophylla var. *beta* Nees, Agrost. Bras. 419. 1829. TYPE: BRAZIL, Nees (B, destroyed; ISOTYPES: possibly in CGE or M).

Chloris bahiensis Steudel, Syn. Pl. Glum. 1:208. 1854. TYPE: BRAZIL. BAHIA, Moricand Hrbr. nr. 2442. (G). *Eustachys bahiensis* (Steudel) Herter, Fl. Ilustr. Uruguay 1:85. 1941.

Chloris bahiensis Steudel forma *glabrescens* Hackel, Repert. Spec. Nov. Regni Veg. 8:46. 1910. TYPE: PARAGUAY. PARAG., septentr. 1909. *Friebrig 4575* (G). *Chloris glabrescens* (Hackel) Roseng. & Iz., Bol. Soc. Argent. Bot. 12:123. 1968. *Eustachys glabrescens* (Hackel) Caro & Sanchez, Kurtziana 6:120. 1971.

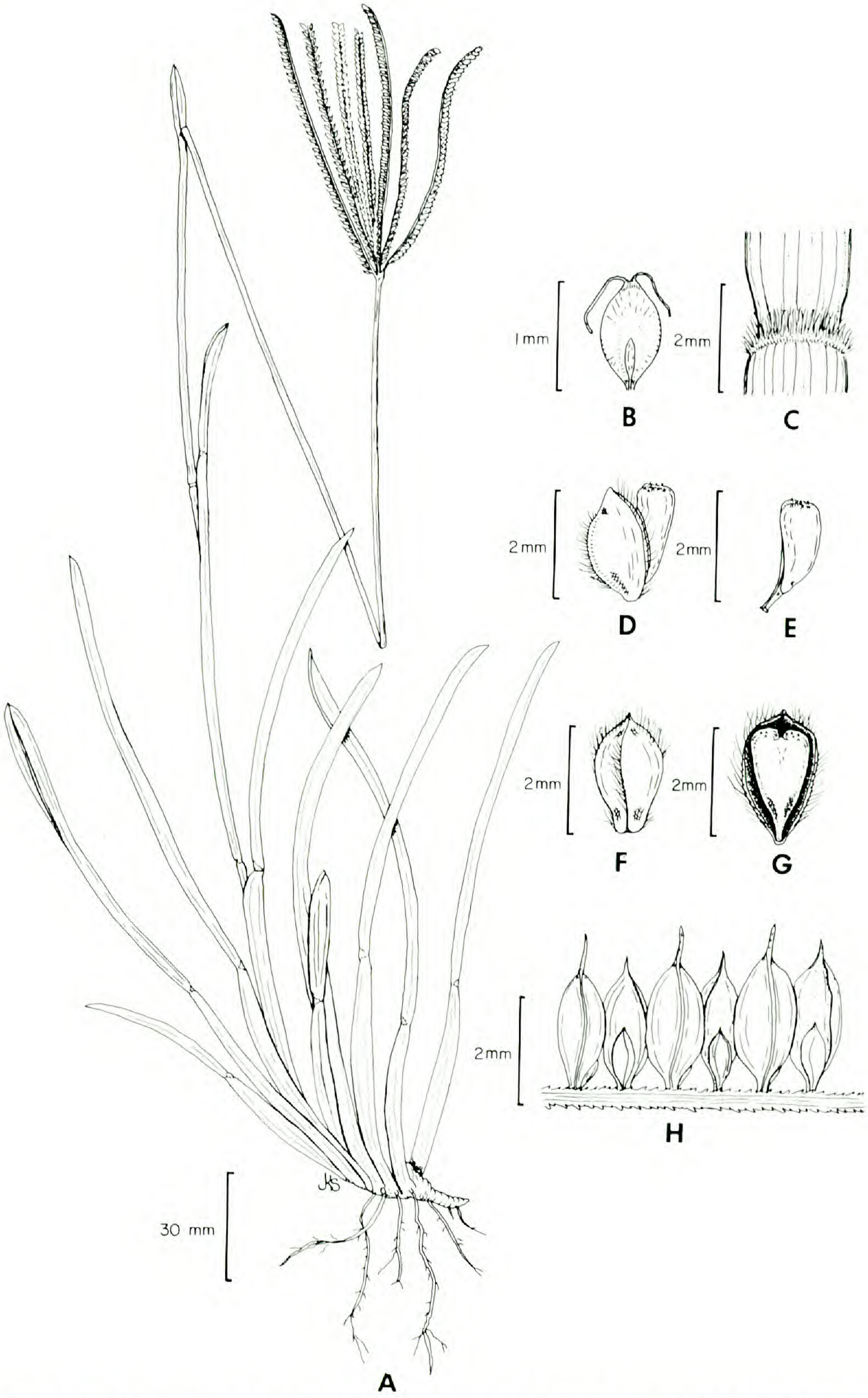

Fig. 1. *Eustachys caribaea*, A. habit; b. grain; C. ligule; D. florets; E. sterile floret; F dorsal view of lemma of fertile floret; G. ventral view of lemma of fertile floret including the sterile floret; H. segment of rachis with spikelets.

Tufted rhizomatous perennial to 0.7 m tall; sheaths sharply keeled, glabrous to sometimes hirtellous along the keel; ligule ciliate, 0.5 – 1.0 mm long, cilia somewhat fused basally forming a short membrane; blades conduplicate, 2 – 22 cm long, 0.6 – 1 cm wide, glabrous to moderately hirtellous, bluish green; spikes 4 – 9 (10), 4 – 9 cm long, strongly ascending, rachis triangular, scabrous along the angles; spikelets in two rows, crowded, ca 21 per cm, 2.0 – 2.5 mm long, lower floret fertile, upper floret sterile, first glume 0.9 – 1.3 mm long, keel midrib green becoming stramineous with age, margins membranous, apex acute, second glume (including awn) 2.0 – 2.4 mm long, keel and margins as in first glume, apex obtusely lobed, awn 0.5 – 0.7 mm long; fertile lemma 2.5 – 3.2 mm long, 1.1 – 1.5 mm wide in side view, strongly keeled, basal or middle one-half to three-fourths of keel and margins pilose with white hairs longer than 0.5 mm, body glabrous, shiny, tawny to reddish brown, apex generally mucronate from slightly below the apex, callus with a few hairs; sterile floret one, 1.2 – 1.5 mm long, ca 0.7 mm wide, obconic, glabrous to puberulent at the truncate apex, same color as fertile lemma; caryopsis ca 1.1 mm long, ellipsoid, triangular in cross section, translucent.

Eustachys caribaea is known from Bolivia, northern Argentina, Paraguay, Uruguay, Brazil from Pernambuco to the Rio Grande do Sul (Cabrera 1970; Smith et al. 1981) and Calcasieu Parish, Louisiana. It grows in disturbed sites along roadsides, in cleared fields and around dwellings. In its native habitat it flowers from September to May. In the U.S. it was flowering when observed in April 1986 and was also flowering when observed in July and September, 1985. Its common name is reported to be "capim-pe-de-galinha," chicken foot grass, by Smith et al. (1981). Specimens (*McKenzie 65 & 114*) are deposited in FLAS, KNK, LAF, LSU, NLU, TAES, US, and USCH.

EXCLUDED NAMES

ANDROPOGON CAPENSE Houtt., Nat. Hist. II. 13: Aanwyz. Plaat. [2] pl. 103 f. 3. 1782. *Chloris capensis* (Houtt.) Thell., Repert. Spec. Nov. Regni Veg. 10:289. 1912. *Eustachys capensis* (houtt.) Chiov., Webbia 8:115. 1951. *Chloris capensis* var. *bahiensis* (Steudel) L. Parodi, Rev. Agr. Agron. 20:26. 1953. *Chloris capensis* var. *glabrescens* (Hackel) L. Parodi, Rev. Agr. Agron. 20:26. 1953.

CHLORIS PENDULA Salzm. ex Steud., Syn. Pl. Gram. 1:208. 1854. pro. syn.

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ADDITIONS TO THE VASCULAR FLORA OF OKLAHOMA—IV

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ABSTRACT

The following thirty taxa are being reported new to Oklahoma: *Amaranthus gracilis* Desf., *Amorpha nana* Nutt., *Apium leptophyllum* (Pers.) Muell., *Astragalus leptocarpus* T. & G., *Botrychium biternatum* (Sav.) Underw., *Cardamine angustata* O.E. Schulz var. *multifida* (Muhl.) Ahles, *C. a.* var. *ouachitana* E.B. Smith, *Carex digitalis* Willd., *Croton argyranthemus* Michx., *Erianthus ravennae* (L.) Beauv., *Euphorbia exstipulata* Engelm., *Geranium texanum* (Trel.) Heller, *Helianthus decapetalus* L., *Hordeum leporinum* Link, *Melica altissima* L., *Myagrum perfoliatum* L., *Pinaropappus roseus* (Less.) Less., *Poa canbyi* (Scribn.) Piper, *Potentilla paradoxa* Nutt., *Rubus invisus* (Bailey) Britt., *Rumex conglomeratus* Murr., *Salsola collina* Pall., *Scirpus fluviatilis* (Torr.) Gray, *Sisyrinchium minus* Engelm. & Gray, *Solidago auriculata* Shuttleworth, *Solidago wrightii* Gary var. *adenophora* Blake, *Utricularia radiata* Small, *Uvularia perfoliata* L., *Vicia exigua* T. & G., *Vaccinium fuscatum* Ait., and *Gentiana puberulenta* Pringle are documented as occurring in Oklahoma. The type of *Dalea phleoides* (T. & G.) Shinners var. *phleoides* is most likely from Oklahoma.

INTRODUCTION

Results of field work and herbarium studies at Durant indicate not only the continued introduction of weedy species into the state of Oklahoma, but that many habitats have not yet been sufficiently collected. The following taxa are believed to be new to Oklahoma, or if listed, no specimen verification was given. Specimens are located at DUR with duplicates of most at SMU unless otherwise indicated. Taxa are in phylogenetic order.

BOTRYCHIUM BITERNATUM (Sav.) Underw. **Leflore Co.**: woods near stream at base of north side of Blue Bouncer Mt., 11 mi NE of Octavia, 14 Sep 1968, *J. & C. Taylor 4993*. **McCurtain Co.**: floodplain of Little River, 6 mi S of Broken Bow, 27 Apr 1974, *J. & C. Taylor 15967*; Carter Creek area near Glover River, 10.5 mi S of Battiest, 12 Apr 1972, *J. & C. Taylor 10032*. Specimens determined by David M. Johnson.

ERIANTHUS RAVENNAE (L.) Beauv. **Cleveland Co.**: west edge of Norman near I35, in floodplain of South Canadian River, 15 Nov 1981, *J. & C. Taylor 31208*. **McCurtain Co.**: roadside ditch, 5.5 mi S of Idabel along Hwy 259, 0.5 mi N and 1 mi W of Shawnee Town road, 13 Aug 1984, *J. & C. Taylor 32520*.

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HORDEUM LEPORINUM Link. **Bryan Co.**: growing as a lawn weed on Southeastern Oklahoma State University campus, 3 May 1981, *J. Taylor 30083*.

MELICA ALTISSIMA L. **Comanche Co.**: granite knob, 1.6 mi W of jct Ok Hwy 49 and US Hwy 281, just E of entrance of the Wichita Mts. National Wildlife Refuge, 23 Apr 1981, *J. & C. Taylor 29881*; on top of Mt. Scott in above refuge, 2 May 1976, *J. & C. Taylor 21136* (dupl. det. H.E. Ahles). **Greer Co.**: rock quarry on N edge of Granite, 25 Apr 1981, *J. & C. Taylor 29933*. **Jackson Co.**: granite outcrop about 2 mi NE of Headrick near North Fork of the Red River, 25 Apr 1981, *J. & C. Taylor 30069*.

POA CANBYI (Scribn.) Piper. **Beaver Co.**: along Clearwater Creek, about 4.6 mi N of Elmwood at US Hwy 270 bridge, 9 May 1982, *J. & C. Taylor 31606*. **Woods Co.**: 7.5 mi NW of Alva along a narrow creek, 16 May 1981, *P. Nighswonger 1844*.

CAREX DIGITALIS Willd. **Mayes Co.**: wooded limestone bluff in park below Lower Spavinaw Lake Dam, just S of Spavinaw, 14 Jun 1985, *J. & C. Taylor 33451*. **Osage Co.**: rocky wooded N-facing slope on S side of Sand Creek, 6 mi N of Pawhuska, *J. & C. Taylor 33365*.

SCIRPUS FLUVIATILIS (Torr.) Gray. **Washington Co.**: large pond 0.25 mi S of Copan Dam on Caney River, 13 Jun 1985, *J. & C. Taylor 33279*.

UVULARIA PERFOLIATA L. **McCurtain Co.**: Mountain Fork River, 8.4 mi NE of Smithville; beech-pine-oak-hickory woods, rare on N-facing slope, 4 Apr 1982, *L.K. Magrath 12564* (DUR, OCLA). This plant has petals that are papillose within and less than 2.5 cm long; the leaves are very glaucous. It is closely related to *U. grandiflora* Sm. which has been collected from numerous locations.

SISYRINCHIUM MINUS Engelm. & Gray. **Bryan Co.**: lawn weed on campus of Southeastern Oklahoma State University, 26 Apr 1981, *J. Taylor 30077*.

SALSOLA COLLINA Pall. **Cimarron Co.**: sandy floodplain of Beaver River, 18.5 mi SW of Boise City, 29 Jul 1981, *J. & C. Taylor 30927*.

AMARANTHUS GRACILIS Desf. **Bryan Co.**: garden weed, 6.5 mi SE of Durant, 1 Aug 1983, *J. Taylor 32067*.

RUMEX CONGLOMERATUS Murr. **Choctaw Co.**: wet area 0.5 mi S of Hugo Dam on Kiamichi River, 28 Jun 1983, *C. Taylor 31912*. **McCurtain Co.**: Beavers Bend area of Mountain Fork River, 25 May 1977, *J. Taylor 24384B*; limestone bluff along Little River at Goodwater Crossing, 17.7 mi NE of Idabel, 20 May 1978, *J. & C. Taylor 26167*.

CARDAMINE ANGUSTATA O.E. Schulz var. MULTIFIDA (Muhl.) Ahles. **McCurtain Co.**: behind Broken Bow Dam, 20 Mar 1977, *M. Parham s.n.*; Stevens Gap area of Beavers Bend State Park, 30 Mar 1978, *A. Crain 13*;

NW corner of Beavers Bend State Park, 7 mi N & 3 mi E of Broken Bow, 30 Apr 1978, *J. Taylor 25911*.

CARDAMINE ANGUSTATA O.E. Schulz var. OUACHITANA E.B. Smith. **McCurtain Co.**: Jones Crossing on Glover River, 10.5 mi S of Battiest, 24 Mar 1972, *J. & C. Taylor 9818*; 1 mi S of Zafra, 21 Mar 1981, *M. Bailey 39*.

MYAGRUM PERFOLIATUM L. **Bryan Co.**: 4.5 mi E, 1.5 mi S of Caddo in old field, 26 Mar 1971, *K. Snider 31*.

POTENTILLA PARADOXA Nutt. **Cimarron Co.**: west shore of Lake Carl Etling, about 25 mi NW of Boise City, 9 May 1982, *J. & C. Taylor 31532*. **Woods Co.**: 7.5 mi NW of Alva at margin of stock pond, 3 Jul 1981, *P. Nighswonger 1851*.

RUBUS INVISUS (Bailey) Britt. **Ottawa Co.**: north-facing wooded limestone slope along US Hwy 60, 5 mi W of Oklahoma state line, and just E of its jct with OK Hwy 10, 14 Jun 1985, *J. & C. Taylor 33405*.

AMORPHA NANA Nutt. **Comanche Co.**: near summit of Mt Scott in the Wichita Nountains National Wildlife Refuge, 24 Apr 1981, *J. & C. Taylor 29884*.

ASTRAGALUS LEPTOCARPUS T. & G. **Atoka Co.**: Antlers sand near Boehler, 14 Apr 1975, *J. Taylor 18230*; 6 May 1975, *J. Taylor 18431*; 14 Apr 1978, *L. Luman 82*. **Marshall Co.**: sandy hills adjacent to Lake Texoma, 2.5 mi E, 0.4 mi S of Enos, 29 May 1985, *J. & C. Taylor, E. Bridges, & S. Orzell 33168*. **Pushmataha Co.**: Antlers (Harrison) Bog, 5.5 mi W of Antlers, 1 May 1977, *J. Taylor 24114*; 21 May 1981, *J. Taylor & L. Magrath 30177*, (DUR, OCLA); 1 May 1982, *L. Magrath 12706* (DUR, OCLA).

DALEA PHLEOIDES (T. & G.) Shinners var. PHLEOIDES. Eastern Oklahoma was originally a part of Arkansas Territory. This has created confusion about the location of some older specimens. *Dalea phleoides* seems to be one of these. While Wemple (as *Petalostemon phleoides*, 1970) shows this species as endemic to east Texas, and Barneby (1977) does not dispute his distribution, the specimen of Leavenworth indicated as a type (NY) is from "Arkansas" (Torrey & Gray, 1842). Dr. Leavenworth was stationed at Ft. Towson and Ft. Washita both then in Arkansas Territory, but presently a part of Oklahoma and located over 50 and 80 miles west of the Arkansas state line. Both are in counties adjacent to the Red River and thus the Texas state line. The type specimen most probably is from Oklahoma, perhaps Choctaw County in the vicinity of Ft. Towson.

VICIA EXIGUA T. & G. **Cimarron Co.**: rocky canyon at east end of Black Mesa (Mesa de Maya) 3 mi N of Kenton, 8 May 1982, *J. & C. Taylor 31513*.

GERANIUM TEXANUM (Trel.) Heller. **Jackson Co.**: 7 mi NE of Eldorado in gypsum capped escarpments, 4 May 1985, *J. & C. Taylor 33007*. **McCurtain Co.**: Barney Ward Lake, 1 mi E and 0.5 mi S of Tom, 4 Jun 1976, *J. & C. Taylor 21587*.

CROTON ARGYRANTHEMUS Michx. **Kiowa Co.**: sandy area along E side of the North Fork of the Red River, 3 mi NE of Headrick, 8 Jul 1976, *J. Taylor 21498*.

EUPHORBIA EXSTIPULATA Engelm. **Cimarron Co.**: rocky canyon about 0.75 mi SE of Kenton, 10 Aug 1977, *J. & C. Taylor 25179*. **Murray Co.**: Cowpen Canyon, 2 mi above its jct with Honey Creek, 4 Jun 1977, *J. & C. Taylor 24521*. Both specimens were determibned by G.L. Webster.

APIUM LEPTOPHYLLUM (Pers.) Muell. [*Ciclospermum leptophyllum* (Pers.) Sprague]. **Bryan Co.**: weed in lawn of Southeastern Oklahoma State University campus, 26 Apr 1981, *J. Taylor 30074*. **McCurtain Co.**: along small creek 4 mi E and 3.9 mi S of Idabel, 29 Oct 1975, *J. Taylor 21002D*.

VACCINIUM FUSCATUM Ait. **Choctaw Co.**: mesic forest seep, 1.5 mi E, 3.5 mi N of Swink, 25 Apr 1976, *J. & C. Taylor 21191*; 28 May 1985, *J. & C. Taylor, E. Bridges, S. Orzell 33149*.

GENTIANA PUBERULENTA Pringle. **Delaware Co.**: ca 3.1 mi E and 4.5 mi N of Grove on OK Hwy 10, prairie hay meadow with "pimple" mounds, *L.K. Magrath 10717* (DUR, OCLA). **Rogers Co.**: ca 1.7 mi S of Foyil on US Hwy 66; prairie hay meadow, flowers blue, *L.K. Magrath 10758* (DUR, OCLA). This species was originally reported as *G. puberula* Michx. by Lahman (1931) from Delaware County. No specimens, however can be located, and Waterfall (1969) did not include this species. The elusive plant has now been documented by L. K. Magrath from the above two locations in Oklahoma. The specimens of Lahman were noted as being only one flowered, while those of Magrath have many flowers per stem.

UTRICULARIA RADIATA Small. **Pushmataha Co.**: Mather's Wilderness, ca 10 mi E of Hwy 144, and 0.4 mi S of Nashoba School, 5 Jul 1985, *L.K. Magrath & C.M. Mather 16301* (DUR, OCLA). This species is closely related to *U. inflata* Small.

HELIANTHUS DECAPETALUS L. **Bryan Co.**: growing in wet area near Durant High School in Durant, 6 Aug 1981, *J. Taylor 30943*.

PINAROPAPPUS ROSEUS (Less.) Less. **Greer Co.**: Camp Kate Girl Scout Camp, 3 mi NW of Granite, 25 Apr 1981, *J. & C. Taylor 29953*. **Harmon Co.**: rock gypsum soil, 2.5 mi W and 5.5 mi S of Hollis, 25 Apr 1981, *J. & C. Taylor 30049*. **Jackson Co.**: 7 mi NE of Eldorado, gypsum capped escarpments, 4 May 1980, *J. & C. Taylor 33040*.

SOLIDAGO AURICULATA Shuttleworth. **McCurtain Co.**: rare on densely wooded limestone ledge adjacent to the Little River at Goodwater cross-

ing, 16 mi E and 3 mi N of Idabel, 31 May 1985, *J. & C. Taylor, E. Bridges, & S. Orzell 33192*; 12 Oct 1985, *J. & C. Taylor 33650*.

SOLIDAGO WRIGHTII Gray var. ADENOPHORA Blake. **Cimarron Co.**: rocky side branch of Tesequite Canyon, 25 Sept 1978, *J. Taylor 23699*; rocky canyon about 5 mi N of Kenton, 25 Sep 1976, *J. Taylor 23743*; Signature Rock area, 7 mi W and 5.5 mi N of Boise City, 11 Aug 1977, *J. & C. Taylor 25251*. Reported as *S. petiolaris* in Taylor & Taylor (1984) from which it differs by having smaller (1.5 mm) achenes. This species occurs in the pinyon pine zone and all specimens are from the very NW corner of Oklahoma.

ACKNOWLEDGMENTS

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NOTICE

The 37th Annual Wildflower Pilgrimage will be held in Gatlinburg, Tennessee, the Great Smoky Mountains National Park, and surroundings, on April 23, 24, and 25, 1987. The Pilgrimage is organized and conducted by the Botany Department of the University of Tennessee, Great Smoky Mountains National Park, The Gatlinburg Garden Club, and the Southern Appalachian Botanical club.

Trail hikes, motorcades, photographic tours, flower identification workshops, and photography workshops, under expert leadership, take you to areas where spring wildflowers grow in quality and variety. Morning bird walks and all day birding events are a feature of each day's activities. Special trips are devoted to observations of insects, spiders, salamanders, geological phenomena, and pest species which threaten mountain forests.

An overnight trail hike to Mt. LeConte is scheduled for 24 April. Spaces available at LeConte Lodge require advanced reservations, with a $46.33 deposit. Arrangements should be made directly with the Lodge, telephone (615) 436−4473. Also, an overnight backpacking trip to Spence Field is scheduled for 25 April. Sleeping bags, food, and cooking gear are required.

There is an illustrated talk each evening. Saturday evening's talk features individual participation. You may show ten of your own nature slides.

Registration begins 7:30 a.m. Thursday, 23 April, in the Gatlinburg Civic Auditorium. The fee is $5.00 per day for general registration and $3.00 per day for students. Advanced registrations are not accepted, though large groups are encouraged to contact Ms. Jane Dean, (615) 436-7611 in advance. A detailed description of Pilgrimage events is furnished each participant at registration.

For additional Pilgrimage information write or call Great Smoky Mountains National park, Gatlinburg, TN 37737, telephone (615) 436−5615. If you wish a Gatlinburg Accomodations Directory, dial (toll-free, except in TN) 1−800−251−9868, or write Dept. W.P., Box 257, Gatlinburg, TN 37738.—Submitted by: *Dr. Edward E.C. Clebsch, Department of Botany, University of Tennessee, Knoxville, TN 37996-1100, Tel. 615/974-6209.*

SIDA 12(1): 238. 1987.

LEAVENWORTHIA TEXANA (BRASSICACEAE), A NEW SPECIES FROM TEXAS

WM. F. MAHLER

SMU Herbarium, Dallas, TX 75275, U.S.A.

Leavenworthia texana, occurring only in San Augustine County, Texas, has been passing under the name of *Leavenworthia aurea* Torr. (TYPE: near Ft. Towson, Oklahoma, *Leavenworth s.n.* (HOLOTYPE: NY; ISOTYPE: GH). With the segregation of this taxon, endemic to Texas, *L. aurea* becomes endemic to Oklahoma.

LEAVENWORTHIA **texana** Mahler, sp. nov. Fig. 1.

Leavenworthia petalis anguste obovatis, stylis fructificantibus 2 – 3.5 mm longis, segmentis terminalibus foliorum plerumque latioribus quam longioribus et dentatis vel angularibus.

TYPE: pasture seepage areas on ironstone rock in shallow soil from eroding calcareous Weches formation, 1.5 mi E of San Augustine on Hwy 21, 22 Mar 1987, *Wm. F. Mahler & Elizabeth E. Lyons 10020* (HOLOTYPE: SMU; ISOTYPES: DUR, GH, MO, NY, voucher specimens from population genetic studies by E.E. Lyons: F).

It was unfortunate that Rollins (1956, 1963) was unable to relocate the *Leavenworthia* populations in the vicinity of San Augustine, Texas when he was studying the genus. He would have discovered that these populations have a chromosome number of $2n = 22$ (E.S. Nixon, pers. comm.) and thus, could have helped to substantiate the closeness to *L. exigua* Rollins var. *lutea* Rollins ($2n = 22$, 1963) with which he associated the Oklahoma populations of *Leavenworthia aurea* ($2n = 48$, Rollins 1963). In comparing the living specimens, he also would have noticed the uniformly bright yellow petals (fading at the tips in aging) of the Texas populations and toothed terminal blade segments.

The Oklahoma and Texas populations possess siliques with thickened margins and styles 2 – 3.5 mm long distinguishing these populations from *L. exigua* var. *lutea*, which have thin-margined siliques and styles 1 – 2 mm long (Rollins 1963).

1. Petals bright yellow with slightly darker bases, narrowly obovate; apical leaf segments usually wider than long and toothed or angled . . . . . 1. *L. texana*
1. Petals pale yellow with bright yellow bases, obcordate; apical leaf segments essentially unlobed and orbicular in outline . . . . . 2. *L. aurea*

SIDA 12(1): 239 – 242. 1987.

Fig. 1. *Leavenworthia texana*, ca 1 × (*Mahler & Lyons 10020*).

1. LEAVENWORTHIA TEXANA Mahler is found on the calcareous Weches fossil formation outcrops which cover the surface of the ironstone. This localized endemic is restricted to the treeless glades near San Augustine and is known only from San Augustine County, Texas.

The Texas populations (*L. texana*) may be distinguished from the Oklahoma populations by the narrowly obovate, rather uniformly bright deep yellow petals with only slightly darker yellow bases, and the wider than long terminal leaf segments usually distinctly lobed (Fig. 1). The older petals also may have white tips indicating a close relationship to *L. aurea*.

The illustration of *L. aurea* in Mahler (1981, Fig. 6) is evidently that of

Fig. 2. *Leavenworthia aurea*, ca 1 × (*Mahler 10019*).

L. texana. The narrowly obovate petals and the terminal leaf segment that is slightly wider than long and angularly toothed are characteristics of *L. texana*. However, most of the terminal leaf segments are distinctly wider than long with prominent teeth (Fig. 1). In that study, the Oklahoma and Texas populations were regarded as the same species. Not long after the study, Nixon and Hoff (pers. comm.) obtained chromosome counts of $2n = 22$. A study of the 35 mm Kodachrome slides from the Texas and Oklahoma populations prompted additional field work in the spring of 1987 with Elizabeth Lyons, John and Connie Taylor, and Elray Nixon.

2. LEAVENWORTHIA AUREA Torr. is a weedy pioneer species occupying

disturbed areas and is restricted to the shallow, moist limestone soils of the Washita group from Hugo (Choctaw County) to near the Arkansas state line in McCurtain County (Mahler 1980, 1981).

The Oklahoma populations (*L. aurea*) have obcordate, pale or lemon yellow petals with whitish tips and bright yellow bases and terminal leaf segments essentially orbicular and scarcely angled (Fig. 2.).

ACKNOWLEDGMENTS

I am indebted to E.S. Nixon (ASTC), J.C. and C.E.S. Taylor (DUR), and E.E. Lyons (NWU) for their field work and discussions regarding this species and B.L. Lipscomb and A.P. McFadden (SMU). Special thanks to E.S. Nixon and Victor Hoff (ASTC) for the chromosome counts and to P. A. Fryxell (U.S.D.A.) for the Latin diagonsis and comments.

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NOTES

JUNCUS EXILIS OSTERHOUT (JUNCACEAE), AN OVERLOOKED SYNONYM OF *J. CONFUSUS* COVILLE.—Through the courtesy of Meredith Lane, Acting Curator at RM, we recently learned that Professor Roger Williams of the History Department at the University of Wyoming is undertaking to write a biography of George E. Osterhout, an amateur botanist whol collected widely in Colorado and who was a contemporary of Aven Nelson. Professor Williams is attempting to account for the current status of all the vascular plant names published by Osterhout. In his researches, he discovered that *Juncus exilis* Osterhout (Bull. Torrey Bot. Club 57(8):559–560. 1930; holotype from Steamboat Springs, Routt County, Colorado, 11 Jul 1912, No. 4965, RM Acc. No. 170602) is neither accepted in any current treatment of the genus nor given in synonymy. At our request, Lane sent the hologype of *J. exilis* on loan. Examination of it confirms Osterhout's original supposition, that "the species has some likeness to *Juncus confusus* Coville ...." Indeed, it is inseparable from it. (We forbear to comment on the distinctness of *J. confusus* from *J. tenuis* Willd.).

The failure of various workers (Harrington 1954; Weber 1976; Hermann 1975) to cite the binomial in synonymy doubtless stems from the manner in which the type description was composed: most of the characters are given, but differentail, distinguishing characters are not. Only an examination of the holotype could have resolved the identity of the plant. We thank Meredith Lane (RM) for her help in tidying up this nomenclatural point.—*Melanie DeVore and Neil A. Harriman, Biology Department, University of Wisconsin-Oshkosh, Oshkosh, WI 54901, U.S.A.*

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GLAUCIUM FLAVUM CRANTZ (PAPAVERACEAE) AND *SILYBUM MARIANUM* (L.) GAERTN. (ASTERACEAE) IN OKLAHOMA—The meeting of the Annual Wildflower Workshop in

mid-May 1985 called attention to two new naturalized weedy plants in Oklahoma. Vouchers of all specimens cited are located at OCLA.

GLAUCIUM FAVUM Crantz. Specimens of this plant were brought to the work shop by Mrs. Homalene Riggs for identification. Using Komarov (1937) the plants were determined to be *G. flavum* and distinct from *G. corniculatum* (L.) J.H. Rudolph which has recently been reported for Kansas (McGregor et al. 1986). **Tillman Co.**: ca 2 mi N of Fredrick on W side of US 183, locally common, 13 May 1985, *Riggs s.n.*. **Kiowa Co.**: along US 183 just N of Snyder between Hwy and railroad, locally abundant, 13 May 1985, *Riggs s.n.* Fernald (1950) indicates that this plant occurs in the northeastern United States west to Michigan and south to West Virginia.

SILYBUM MARIANUM (L.) Gaertn. This plant was first located in early May 1985 by Dr. Doyle McCoy, and a collection was made in 1986. **Blaine Co.**: 5.5 mi N of Greenfield on US 281, grassy right-of-way between hwy and railroad, scattered, 10 May 1986, *Magrath, McCoy & Harrison 16529*. Britton & Brown (1913) report that this plant occurs from Ontario south to Alabama and also on the Pacific Coast from British Columbia south to southern California, while Fernald (1950) notes that it occasionally escapes from gardens. Correll & Johnston (1970) indicate that this plant is rare and local in the Edwards Plateau of Texas, while McGregor et al. (1986) do not list it for the Great Plains region.—*Lawrence K. Magrath, Discipline of Biology, University of Science & Arts of Oklahoma, Chickasha, OK 73018, U.S.A.*

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NEW AND OTHERWISE INTERESTING PLANTS FROM THE JACKSON PURCHASE AREA OF KENTUCKY—Several state records and other noteworthy plant taxa have been recently collected from the Jackson Purchase area of Kentucky. Floristic information from this portion of the state is relatively limited (Fuller 1979). The following plant species were encountered during field work in several counties in extreme western Kentucky. Nomenclature follows Kartesz and Kartesz (1980). Voucher

specimens cited *Heineke & Woods* are deposited at the Memphis District, Corps of Engineers Herbarium, Memphis, Tennessee; and those cited *Woods & Heineke* are deposited in the herbarium of Murray State University (MUR).

AMORPHA NITENS Boynt. **Carlisle Co.**: along an abandoned railroad bed at the base of loessial bluffs ca 0.5 mi NNE of Laketon, 2 May 1986, *Heineke & Woods 3808*. **Ballard Co.**: bordering a bald cypress slough in the Ballard State Wildlife Management Area, 19 Jul 1986, *Woods & Heineke 5961*. A specimen of this taxon (*Smith & Hodgdon 4216*) from Marshall Co., Kentucky, is deposited at the United States National Herbarium (US).

The distribution for this species is Georgia to Arkansas and north to southern Illinois (Fernald 1950). Although this is the first report of this species in Kentucky, it seems likely that *A. nitens*, based on its known range, will be found with some regularity in extreme western Kentucky.

CARYA TEXANA Buckl. **Calloway Co.**: on a sandy, wooded slope with *Quercus velutina* Lam., *Q. stellata* Wang., and *Nyssa sylvatica* Marsh., off Hwy 280 E, ca 1 mi E of Hwy 121, 2 Jul 1986, *Woods & Heineke 5927*. Although Kentucky lies within the range of this species (Louisiana and Texas, north to southern Indiana, southern Illinois, Missouri, and eastern Oklahoma (Fernald 1950)), it has previously not been reported for the state. This species has likely been overlooked in the past and probably occurs in much of the Jackson Purchase area where suitable habitat exists.

CENTAUREA CYANUS L. **Calloway Co.**: along the edge of a sandy upland woods off Hwy 280 E, ca 0.1 mi W of Murray State University Golf Course, 3 May 1986, *Woods & Heineke 5890*. This non-native species is reported for the first time in Kentucky.

CAREX BAILEYI Britt. (! R.H. Mohlenbrock). **Hickman Co.**: on the edge of a marsh/shrub-swamp/swamp complex at Murphy's Pond, 7 Jun 1986, *Woods & Heineke 5904*. This rare sedge was previously known from Bell, Harlan, and Letcher counties of Kentucky (Beal & Thieret unpubl. ms.), some 300 miles to the east of this station.

CAREX SOCIALIS Mohlenbrock & Schwegm. (! R.H. Mohlenbrock). **Hickman Co.**: in bottomland hardwoods at Murphy's Pond, 7 Jun 1986, *Heineke & Woods 3872*. This sedge was previously known for Kentucky from Ballard and Livingston counties (Harker et al. 1980). This species is known from Arkansas, Illinois, Indiana, Kentucky, Missouri, and Tennessee (Federal Register 1985) and has been given the status of "threatened" by Harker et al. (1980).

OENOTHERA PERENNIS L. **Calloway Co.**: along a sandy roadside near

the edge of some upland woods in Crappie Hollow Estates, 2 Jul 1986, *Heineke & Woods 3930*. Originally known for Kentucky from a single collection from McCreary County in 1938 (Evans 1986), this perennial evening primrose was rediscovered some 300 miles to the west. Harker et al. (1980) give this species a status of "endangered."—*Thomas E. Heineke and Michael Woods, Department of Botany, SIU-Carbondale, Carbondale, IL 62901, U.S.A.*

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POLYGONUM PERFOLIATUM L. (POLYGONACEAE): A SIGNIFICANT NEW WEED IN THE MISSISSIPPI DRAINAGE.—*Polygonum perfoliatum* L. (Polygonaceae) is a rambling, annual vine in the section *Echinocaulon*. The wiry stems are armed with a multitude of small, but annoying, recurved prickles. The plants form tangled mats over shrubbery and climb several meters into trees, shading out herbaceous and woody vegetation beneath. Thick masses of this vine overwhelm even such aggressive species as Japanese honeysuckle (*Lonicera japonica* L.). *Polygonum perfoliatum* is native to a wide area of eastern Asia from Japan to the Philippines. It is a major agricultural pest throughout its homeland. The species usually is cited as *Polygonum perfoliatum* L., following Steward's broad concept of the genus (1930). Other names in use include *Tracaulon perfoliatum* (L.) Greene (Reed 1979a, b) and *Persicaria perfoliata* (L.) Gross (Ohwi 1965). This species is not listed in Gleason & Cronquist (1979) and is mentioned by Fernald (1950) only as an afterthought to the generic treatment. The Japanese colloquial name of this species is "ishimakawa" (Walker 1976). An appropriate English name might be "giant climbing tearthumb."

In North America, *Polygonum perfoliatum* first was collected in 1890 in Oregon. Apparently the species was a waif on ballast and failed to establish itself in the area. *Polygonum perfoliatum* appeared in a nursery in York County, Pennsylvania in the mid 1930's, possibly having been introduced accidentally with seeds of oriental *Ilex* species. Riefner (1982) provides a capsule history of *P. perfoliatum* in North America.

Giant climbing tearthumb is now well-established in riverine habitats in the lower Potomac and Susquehanna River drainages in York County, Pennsylvania, the District of Columbia, and 11 counties of Maryland (Brown & Brown 1984; Reed 1979a, b; Riefner 1982; Riefner & Windler 1979; Wherry et al. 1979). In these areas it has become a local pest as common as Japanese honeysuckle. *Polygonum perfoliatum* has been reported from the Potomac drainage as far west as Mineral County, West Virginia (Duppstadt 1981). It is as yet uncommon in the westernmost part of its range.

Polygonum perfoliatum also grows in Wood County, West Virginia, at least 150 miles west of the Mineral County populations. This paper is the first to report this weedy species from the Mississippi drainage. Giant climbing tearthumb is locally common along the C. & O. Railroad in the Ohio River Valley north of the small town of Boaz. The species was first collected at this site 18 Oct 1980, *W. Grafton s.n.* (WVA). At that time, the population was limited to two isolated patches, one about 100 ft long and another 150 ft long, separated by about one-fourth mile (W. Grafton, pers. comm. 1985). By 1985 discontinuous colonies were found along about a 3 km stretch of the railroad. Collections were made from various segments of the population on 21 July and 23 Oct 1985, *Cusick 24558, 24959, 24965, 24977 & M. Ortt* (F, KE, MICH, MU, NCU, NY, VDB, WVA). In 1985 the plants bloomed and fruited prolifically from late July to frost.

At the Boaz site *Polygonum perfoliatum* grows in full sun or semi-shade on low shrubbery and young trees at the base of the railroad embankment and at the edge of disturbed woods dominated by silver maple (*Acer saccharinum* L.). *Polygonum perfoliatum* also grows in a recent clearing beside a gas well. A single isolated plant was seen along the weedy shore of the Ohio River nearby. The authors have searched a considerable stretch of both the railroad and the Ohio River in West Virginia and adjacent Ohio without finding additional populations of this species.

It is interesting to speculate how giant climbing tearthumb might have been introduced to the Ohio River Valley. The eastern populations can be

traced to contaminated nursery stock and to dispersal by water. Although the large, blue fruits of *P. perfoliatum* are buoyant and well adapted for hydrochory, water-borne dispersal to the Boaz site is unlikely. The railroad seems a more obvious means of introduction. The species grows on railroad embankments in eastern Maryland (Reed 1979b). However, there is no direct link between the C. & O. Railroad and the Potomac River populations of *P. perfoliatum*. The nearby gas wells are another possible source of introduction. The seeds might have been conveyed in mud on drilling equipment. All explanations remain speculative, of course, unless the Boaz site can be compared with other, so far unknown, populations.

Polygonum perfoliatum is a noxious pest in both its native and its North American ranges. The potential exists for giant climbing tearthumb to spread along the natural corridor of the Ohio River. It would be wise to eradicate the Boaz population as soon as possible before another pestiferous weed is added to the spontaneous vascular flora of the Mississippi drainage.

We thank William Grafton, West Virginia University Extension Service, Beckley, and Brian MacDonald, Coordinator, West Virginia Wildlife/Heritage Database, Department of Natural Resources, Elkins for their cooperation and contributions to this article.—*Allison W. Cusick and Marilyn Ortt, Division of Natural Areas and Preserves, Ohio Department of Natural Resources, Columbus, OH 43224, U.S.A.*

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LILIUM MICHIGANENSE FARWELL (LILIACEAE) AND *GENTIANA ALBA* MUHL. (GENTIANACEAE) NEW TO OKLAHOMA

—LILIUM MICHIGANENSE Farwell (Michigan Lily) was discovered during a field ecology class on 18 June 1980 near the campgrounds at the east end of Lake Eucha. The area is partially shaded by an open grove near the foot of a well wooded bluff. The grass was mowed in late summer and burned annually. The clump 20 feet in diameter contained 25 stalks, each with 1 or 2 blossoms. The green heart was clearly visible. Since no house site was located, it is assumed they had spread naturally. In 1983, the Tulsa Water Department expanded their lagoon and the site was buried under tons of soil. A few tubers were saved and continue to flourish in two local gardens. An effort will be made to reinstate the colony beyond the boundary of the lagoon when the area has stabilized. This species is reported to occur in the adjacent counties of southwestern Missouri (Steyermark, Flora of Missouri. 1963) and northwestern Arkansas (Smith, Atlas and Annotated List of the Vascular Plants of Arkansas. 1978).

VOUCHER: U.S.A. **OKLAHOMA. Delaware Co.**: near campgrounds at east end of Lake Eucha, 18 Jun 1980, *M. & F. Baumgartner s.n.* (DUR, OKLA, pers. herb. at Jay).

GENTIANA ALBA Muhl. (Pale Gentian) was first noted on 3 Oct 1981 and has since appeared annually in a remote V-shaped hollow in the Oklahoma Ozarks. About 20 single plants were found at scattered intervals, and later found at two other localities in the ravine. Blooming is from late September to early November, but a few blossoms have been recorded as late as 6 December. Plants are scarce and fail to bloom in dry years. Identification was confirmed by Dr. Larry Magrath and J.L. Norman, who has since found a second location.

VOUCHERS: U.S.A. **OKLAHOMA. Adair Co.**: Tate Ranch, ca 5.2 mi S and W of Chewey, oak-hickory woods in ravine at base of a N-facing slope, 30 Sep 1985, *J. Norman s.n.* (OCLA). **Delaware Co.**: E of ravine near bottom of stream, at Little Lewis Whirlwind Nature School and Sanctuary south of Jay, 3 Oct 1981, *F. & M. Baumgartner s.n.* (DUR, OKLA, and pers. herb. at Jay).

—*Frederick M. and A. Marguerite Baumgartner, Little Lewis Whirlwind Nature School and Sanctuary, Rt. 2, Box 51A, Jay, OK 74346, U.S.A.*

CYPERUS UNIFLORUS (CYPERACEAE) EAST OF THE MISSISSIPPI RIVER—*Cyperus uniflorus* Torr. & Hook. is widespread from Arkansas west throughout much of Texas into New Mexico and Arizona and from northern Mexico northward into Oklahoma (Correll & Johnston, 1970). Previously, it has been reported only once from east of the Mississippi River. This report is based upon a specimen (US, no. 808305) collected in New Jersey by *Kneiskern s.n.* (Horvat 1941); however, because New Jersey is so far out of range for this species Horvat speculated that it originated from ballast or that labels were transposed. Among herbarium specimens examined during systematic studies in *Cyperus* some of *C. uniflorus* from Alabama and Mississippi were found, and these are the basis for this first unequivocal report of the species from east of the Mississippi River.

Collection Data: **ALABAMA. Pickens Co.**: in sandy borrow pit ca 8 mi S of Aliceville, 8 Sept 1968, *R. Kral 33002* (SMU, VDB). **MISSISSIPPI. Bolivar Co.**: ca 2 mi SW of Rosedale, Great River Road State Park, on sandy soil along Mississippi River, 9 Oct 1986, *C.T. Bryson 5083* (IBE, MISSA, SMU, VDB, VSC, ctb-Bryson pers. herb.). **Scott Co.**: sandy clay hilltop, E side of lake at Roosevelt State Park, 2 Jun 1985, *C.T. Bryson 3974* (VSC, ctb-Bryson pers. herb.).

—Richard Carter, Herbarium, Biology Department, Valdosta State College, Valdosta, GA 31698, U.S.A.; Charles T. Bryson, Southern Weed Laboratory, Delta States Research Center, Stoneville, MS 38776, U.S.A.; Barney L. Lipscomb, SMU Herbarium, Dallas, TX 75275, U.S.A.

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NEW COMBINATIONS AND NOTES ON THE NORTH CENTRAL TEXAS FLORA—In revising Shinners' Manual of the Flora of North Central Texas, two new combinations are necessary.

PEDIOMELUM **latestipulatum** (Shinners) Mahler, comb. nov., based on *Psoralea latestipulata* Shinners, Field & Lab. 19:22. 1951.

On rocky or sandy soils; endemic to north central Texas from Grand Prairie westward.

PEDIOMELUM HYPOGAEUM (Nutt.) Rydb. var. **scaposum** (Gray) Mahler,

comb. nov., based on *Psoralea hypogaea* Nutt. var. *scaposa* Gray, Boston J. Nat. Hist. 6:173. 1850.

On limestone; endemic to eastern edge of Edwards Plateau north to Wise County.

Range extensions of two species of orchids have been reported by Dale Williams (Friends of Greenhills 5(5):2, 3. 1986) for Dallas County. *Hexalectris nitida* L.O. Wms. [*Mahler 9993* (SMU); *Bob & Lou Ellen O'Kennon 862* (SMU)] and *H. warnockii* Ames & Correll [*Bob & Lou Ellen O'Kennon 861* (SMU)] are growing among the junipers at the Dallas Nature Center (formerly Greenhills Environmental Center). *Hexalectris nitida* is also currently known from Brewster, Bandera, Kendall, and Taylor counties (Poole, Jackie M, Steve L. Orzell, Comments to U.S. Fish & Wildlife Service, 1987 meeting, Albuquerque, NM). Dallas County is apparently the easternmost edge of the range of these two taxa.—*Wm. F. Mahler, SMU Herbarium, Dallas, TX 75275, U.S.A.*

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TAXONOMY OF *HELENIUM* SECT. *ACTINEA* (ASTERACEAE)

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ABSTRACT

Actinea Juss. is reduced in status to a section of *Helenium* L., and a taxonomic treatment is presented for the three presently recognized taxa: **Helenium radiatum** (Less.) Bierner (= *H. alternifolium* [Sprengel] Cabrera), *H. donianum* (Hook. & Arn.) Cabrera var. *donianum*, and **H. donianum** var. **linearifolium** (Kuntze) Bierner. The latter, which was originally described as a variety of *Actinea heterophylla* Juss. (= *H. radiatum*), has not been recognized as a valid biologic entity since its description. Sectional relationships and sectional disjunctions are also discussed. This treatment takes into account all known morphologic, cytologic, and chemical data.

INTRODUCTION

Helenium L. sect. *Actinea* (Juss.) Bierner comprises three taxa confined to Argentina and Uruguay. Originally recognized as a separate genus (Jussieu 1803), it was treated by Lessing (1832) and Candolle (1836) as a subgenus of *Cephalophora* Cav. (= *Helenium* L. sect. *Cephalophora* [Cav.] O. Hoffm. of Chile and Peru). Later, Hoffmann (1894) and Cabrera (1941) recognized these taxa as part of *Helenium*, but they did not separate them at the subgeneric level.

For many years the names *Actinea* and *Actinella* Pers. (a superfluous name for the former) were applied to a large number of taxa in both South and North America that are now placed in the closely related genus *Hymenoxys* Cass. (including *Tetraneuris* E. Greene). However, the type species, *Actinea heterophylla* (= *Helenium radiatum*), unquestionably belongs to *Helenium*.

SECTIONAL RELATIONSHIPS

The taxa of South America originally described in *Actinea* and *Cephalophora* (excluding those that belong to *Hymenoxys*) generally have been recognized as congeneric with *Helenium* (Hoffmann 1894, Cabrera 1941, Bierner 1971), but until recently (Bierner 1978 and this paper), no effort was made to separate them into distinct sections of *Helenium*. Lessing (1832) and Candolle (1836), however, treated the taxa of *Cephalophora* and *Actinea* (the latter as *Actinella*) as congeneric and separated them at the infrageneric level, but they recognized *Cephalophora* as a genus distinct from *Helenium*.

SIDA 12(2):253–271. 1987.

Geographically, sect. *Actinea* and sect. *Cephalophora* are separated by the Andes, which no doubt presents a significant barrier to gene exchange. In fact, I have observed no specimens in the field or herbarium that suggest any recent contact between the two sections.

Morphologically, these two sections are quite similar, but they consistently can be distinguished by the shape of their pappus scales and several characters in combination (Table I). Morphology of leaves, involucre, receptacle, achenes, corollas, stamens, and styles indicates clearly that the sections are congeneric with *Helenium*.

Cytologic data also support the treatment of *Actinea* and *Cephalophora* as sections of *Helenium*. Both sections have base chromosome numbers of × = 17 (Bierner 1978, Turner et al. 1979), a number that has been suggested to be ancestral for the genus (Bierner 1972). Chromosome numbers of n = 17 are common in the South American taxa, but they are somewhat uncommon among taxa of *Helenium* in North America, having been reported only in *Helenium apterum* (Blake) Bierner (Keil and Stuessy 1977) and *H. scorzoneraefolium* (DC.) A. Gray (Turner et al. 1961) of sect. *Hecubaea*, *H. autumnale* L. of sect. *Helenium* (Darlington and Janaki Ammal 1945, Löve and Löve 1980 and 1982), and *H. pinnatifidum* (Nutt.) Rydb. and *H. vernale* Walt. of sect. *Leptopoda* (Grashoff et al. 1972). Aneuploidy, which is common in North American *Helenium* (Grashoff et al. 1972), is not known in the South American taxa.

Polyploidy reported in *H. donianum* var. *donianum* and *H. radiatum* (Turner et al. 1979) may represent a significant difference between sect. *Actinea* and all other sections of *Helenium*. Thus far, polyploidy has been reported in only one other taxon of *Helenium*, *H. puberulum* DC. ($n = 29$) of sect. *Tetrodus* (Grashoff et al. 1972, Powell et al. 1975, Raven and Kyhos 1961), and this is almost certainly an example of allopolyploidy (Bierner 1972). Counts of both $n = 17$ and $n = 34$ in specimens of *H. donianum* var. *donianum* that I have examined and cannot distinguish morphologically suggest to me that the $n = 34$ plants are autotetraploids. Furthermore, two of the three counts by Turner et al. (1979) in *H. radiatum* are $n =$ ca 34, which suggests that there was some problem with obtaining clear counts. In fact, the chromosome voucher label on one of these specimens, *Sanderson* 356 (TEX), gives the count as $n = 34 + 3$I rather than $n =$ ca 34. This suggests to me that there may be meiotic irregularities and that supernumerary chromosomes are present in at least some populations. This in turn suggests that *H. radiatum* is an autotetraploid taxon of relatively recent origin, or that the plants with gametic chromosome numbers near 34 are spontaneous autotetraploids and plants with $n = 17$ simply have not yet been observed.

Sesquiterpene lactone chemistry also emphasizes the relationship of sects. *Actinea* and *Cephalophora* to the North American sections of *Helenium*. Two taxa of sect. *Actinea* have been examined for sesquiterpene lactones (Herz et al. 1968, Zdero et al. 1986), and both were found to contain helenanolides, which are characteristic of *Helenium* in general (Seaman 1982). Herz et al. (1968) isolated alternilin from *H. radiatum* (as *H. alternifolium* [Sprengel] Cabrera), and brevilin A, tenulin, and linifolin A from *H. donianum* var. *donianum* (mistakenly identified as *H. alternifolium*). Zdero et al. (1986) isolated tenulin, linifolin A, helenalin, microhelenalin C, and several guaianolide glucosides from *H. donianum* var. *donianum* (identification as this taxon confirmed by R. M. King, pers. comm.). Brevilin A has also been isolated from *H. brevifolium* (Nutt.) Wood of sect. *Leptopoda* in North America (Herz et al. 1959), tenulin has been isolated from many taxa in sects. *Amarum, Helenium*, and *Tetrodus* in North America (Seaman 1982), and helenalin has been isolated from sect. *Cephalophora* in South America and from all five sections in North America (Seaman 1982). Linifolin A has been isolated from two species in sect. *Cephalophora, H. aromaticum* (Hook.) Bailey and *H. glaucum* (Cav.) Stuntz (the latter as *H. plantagineum* [DC.] Macbride), and it has also been isolated in North America from *H. scorzoneraefolium* of sect. *Hecubaea* and *H. linifolium* Rydb. of sect. *Tetrodus* (Seaman 1982). In sect. *Cephalophora, H. aromaticum* produces helenalin, mexicanin I, aromaticin, and aromatin, in addition to the linifolin A mentioned preveiously (Seaman 1982). Helenalin is found in all sections of *Helenium* in North America, mexicanin I has been identified in *H. amarum* (Raf.) Rock of sect. *Amarum, H. autumnale* of sect. *Helenium*, and *H. elegans* DC. var. *amphibolum* (A. Gray) Bierner and *H. mexicanum* H.B.K. of sect. *Tetrodus*, and aromaticin has been isolated from *H. amarum* (Seaman 1982). Sesquiterpene lactone chemistry, therefore, indicates that sects. *Actinea* and *Cephalophora* are chemically very similar to the North American sections of *Helenium*.

The flavonoid profiles of sects. *Actinea* and *Cephalophora* (Table II and Fig. 1) are characteristic of *Helenium* in general. Both sections contain methoxylated flavone aglycones (I and V), C-glycosyl flavones (II, III, VI, and VII), methoxylated C-glycosyl flavones (IV and IX), C-di-glycosyl flavones (X and XI), and a number of unidentified minor components; identical compounds have been identified in all of the North American sections of *Helenium* except sect. *Hecubaea*, which has not yet been examined for flavonoids (Bierner 1973).

The morphologic, cytologic, and chemical data provide substantial evidence that sect. *Actinea* and sect. *Cephalophora* are related to one another and are congeneric with *Helenium*. At the same time, these two sections are

geographically isolated and are as morphologically distinct (Table I) as the North American sections are from one another (Bierner 1972).

SECTIONAL DISJUNCTIONS

It is not clear how sects. *Actinea* and *Cephalophora* came to be disjunct from the North American sections and from each other. Greater species diversity in North America suggests that *Helenium* was introduced from North to South America (Bierner 1971), and the most likely mechanism for this amphitropical disjunction is long-distance dispersal (Raven 1963).

It is possible that *Helenium* was introduced once into South America and then was dispersed across the Andes. It is my opinion, however, that the evidence does not support this view. First, these sections are fairly distinct morphologically. Second, the autopolyploidy in sect. *Actinea* is unique in

TABLE I. Characteristics of *Helenium* sections - South America

sect. *Actinea*	sect. *Cephalophora*
1. All three taxa perennial	1. Only one of eight taxa distinctly perennial
2. All taxa radiate	2. Three of eight taxa radiate
3. All taxa without chaff on the receptacle	3. Only one taxon totally without chaff and one usually without
4. Disc corollas 3.3-5.7 mm long	4. Disc corollas (1.6)2.0 − 3.3 mm long in six taxa; 2.9 − 3.6 in *H. vallenariense*; (2.2)2.9 − 4.4 in *H. glaucum*
5. Pappus scales linear to linear-elliptic in *H. radiatum* and *H. donianum* var. *linearifolium*; obovate with a notched apex in *H. donianum* var. *donianum*	5. Pappus scales obovate or obcordate in seven taxa; ovate to obovate to elliptic to lanceolate in *H. glaucum*
6. Pappus scales 2.7 − 5.7 mm long	6. Pappus scales 1.0 − 2.4 mm long in six taxa; 1.7 − 2.9 in *H. urmenetae* var. *urmenetae*; (1.3)1.7 − 3.2(4.1) in *H. glaucum*
7. Outer involucral bracts united in *H. radiatum*; not united to slightly so in *H. donianum*	7. Outer involucral bracts free in all taxa
8. Chromosome numbers n = 17 and 34 in *H. donianum* var. *donianum*; n = 34 in *H. radiatum*	8. Chromosome number n = 17 in seven taxa; *H. insulare* not yet counted

TABLE II. Flavonoids of South American *Helenium*

TAXON	Luteolin 6-OMe (I)	Orientin (II)	Isoorientin (III)	Swertiajaponin (IV)	Apigenin 6-OMe (V)	Vitexin (VI)	Isovitexin (VII)	Isovitexin 7-O-gly? (VIII)	Swertisin (IX)	Vicinin 1 (X)	Vicinin 2 (XI)	Unknown 1 (XII)	Unknown 2 (XIII)	Unknown 3 (XIV)	Unknown 4 (XV)	Unknown 5 (XVI)	Unknown 6 (XVII)	Unknown 7 (XVIII)	Unknown 8 (XIX)	Unknown 9 (XX)	Unknown 10 (XXI)	Unknown 11 (XXII)	Unknown 12 (XXIII)	Unknown 13 (XXIV)	Unknown 14 (XXV)
	Flavonoid																								
Sect. Actinea																									
H. donianum var. donianum	●	●	●	●	●	●	●		●	●	●		●		●		●	●		●	●		●		
H. radiatum	●	●	●	●	●			●	●	●	●	●		●		●		●	●			●			
Sect. Cephalophora																									
H. aromaticum	●	●	●	●	●	●	●		●	●	●								●						
H. atacamense	●	●	●	●	●	●	●				●														
H. urmenetae var. leguiffei	●	●	●	●	●	●	●				●		●				●	●	●	●				●	
H. vallenariense	●	●	●	●	●	●	●		●		●								●	●				●	●

Flavonoids were extracted from midstem leaf material, isolated, and examined spectrally by standard procedures (Mabry et al. 1970). Compounds I through XI were identified by comparing their Rf values, color characteristics, and UV-visible spectral data with those of known coupounds. Unknown compounds are assumed to be identical in different taxa based on Rf values and color characteristics.

Helenium. Third, although the taxa of South America have a base chromosome number of × = 17 and no aneuploidy is present, several taxa in North America do have chromosome numbers of $n = 17$, which is undoubtedly the ancestral base chromosome number for the genus. Fourth, the chemical data do not suggest a closer relationship between sects. *Actinea* and *Cephalophora* than between either of these sections and certain sections in North America. Fifth, *Gaillardia* Foug. and *Hymenoxys*, which are similar to *Helenium* in so many ways, occur only on the east side of the Andes.

It is also possible that *Helenium* was introduced into South America on two separate occasions. *Helenium* sect. *Actinea* appears to be an interior, arid-land, amphitropical disjunct similar in distribution pattern to *Gaillardia* (Turner et al. 1979) and *Hymenoxys* (Turner 1972). *Helenium* sect. *Cephalophora*, however, appears to be a coastal amphitropical disjunct similar in distribution pattern to *Microseris* and *Agoseris*, as discussed by Chambers (1963). This may explain why *Helenium* is on both sides of the Andes while *Gaillardia* and *Hymenoxys* are not. All three genera have taxa

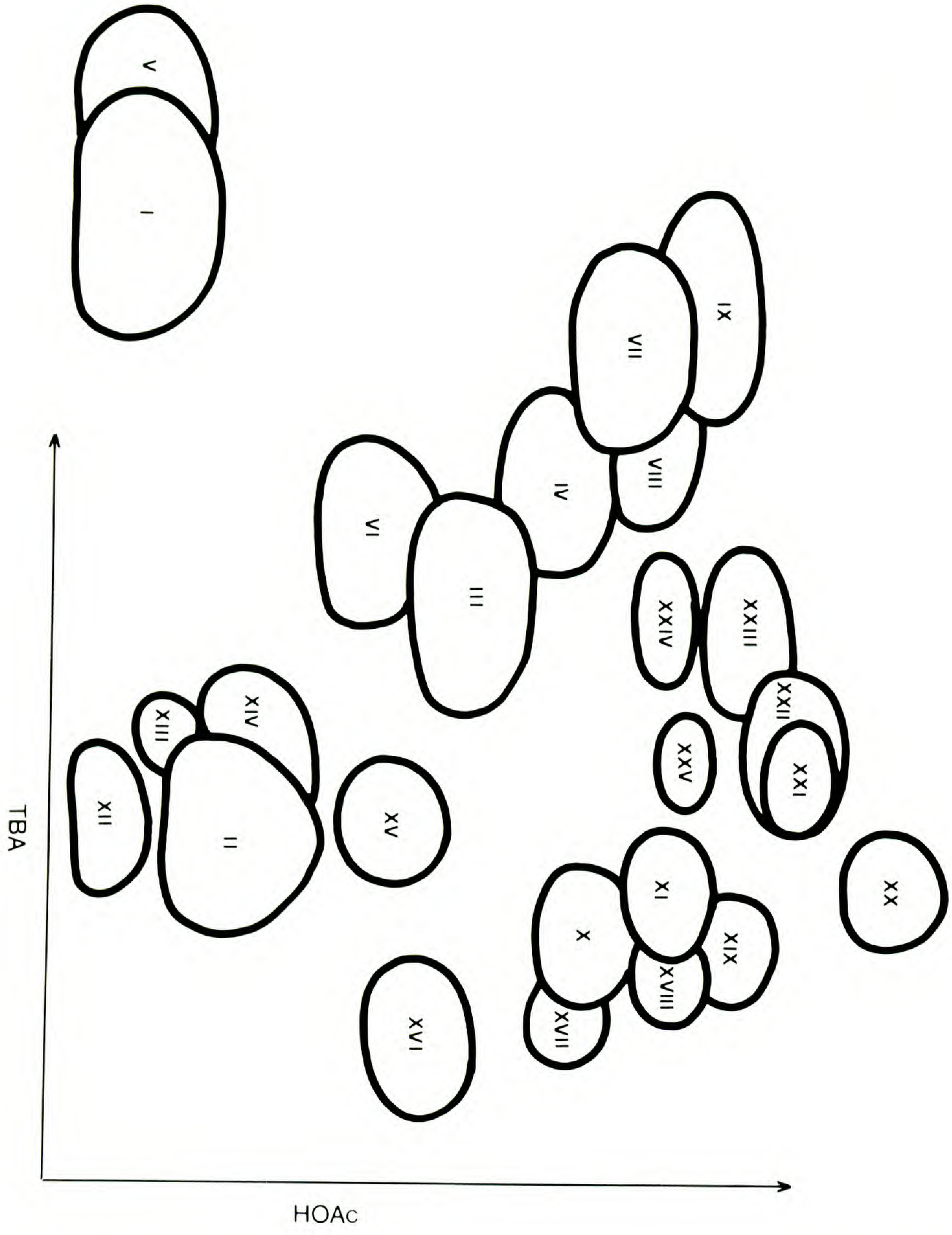

FIG. 1. Composite chromatogram of flavonoid compounds in six taxa of South American *Helenium*. Mid-stem leaf material was extracted overnight in 85% methanol and then spotted on Whatman 3 MM chromatographic paper. Chromatograms were developed in t-butanol, glacial acetic acid, and water (3:1:1 V/V/V) for the first dimension (TBA), and 15% glacial acetic acid for the second dimension (HOAc). Techniques used follow those of Mabry et al. (1970), and compound numbers correspond to those in Table 2.

that range widely across North America, but only *Helenium* (sect. *Tetrodus*) has species that are coastal in northwestern North America. Both sects. *Actinea* and *Cephalophora* appear to be allojunctional in the sense of Turner (1972); that is, the taxa of each section "...have been derived through phyletic divergence from populations now extinct."

In my view, *Helenium* sect. *Actinea* may be phylogenetically most closely related to *Helenium* sect. *Helenium* of North America. Morphologically, *H. donianum* var. *donianum* bears considerable resemblance to some of the populations of *H. autumnale* that have fairly narrow, almost entire leaves, such as plants that have been called *H. autumnale* var. *parviflorum* (Nutt.) Fern. and plants in Virginia that have at times been recognized as a separate species, *H. virginicum* Blake. The broader more dentate leaves of *H. radiatum* are not unlike those of more typical *H. autumnale*. Furthermore, species diversity in sect. *Actinea* and sect. *Helenium* is similar. In the former, only three taxa have developed and they are morphologically very similar; in the latter, while it would not be difficult to recognize at least two species (e.g., *H. autumnale* and *H. virginicum*) and several varieties of *H. autumnale* (e.g., var. *parviflorum* and var. *montanum* [Nutt.] Fern.), the plants are so similar that often *H. autumnale* is recognized as the only taxon in sect. *Helenium*. Also, chromosome numbers of $n = 17$ have been reported for *H. autumnale* (Löve & Löve 1980, 1982).

In sect. *Cephalophora*, the distributions of *Helenium insulare* (Phil.) Cabrera and *H. glaucum* are very similar to those of *H. bolanderi* A. Gray and *H. bigelovii* A. Gray, respectively, of sect. *Tetrodus* (Bierner 1972, 1978). Also, the distribution of sect. *Tetrodus* from the mesic northwestern United States to the arid southwestern United States and arid northern and central Mexico is similar to the distribution of sect. *Cephalophora* from mesic southwestern Chile to the Atacama desert in the north. Furthermore, sect. *Cephalophora* is morphologically quite similar to sect. *Tetrodus*, and evolutionary diversity in both sections is similar. I have recognized 14 taxa in sect. *Tetrodus* (Bierner, 1972) and eight taxa in sect. *Cephalophora* (Bierner 1978), but, depending on ones propensity toward "lumping" or "splitting," fewer taxa could be recognized in the former and more could be recognized in the latter. Both *H. bolanderi* and *H. bigelovii* have chromosome numbers of $n = 16$, but if these sections are truly allojunctional, ancestral populations in North America with $n = 17$ may now be extinct.

TAXONOMY

HELENIUM L. sect. **actinea** (Juss.) Bierner, stat. nov. *Actinea* Juss., Ann. Mus. Natl. Hist. Nat. [Paris] 2:423, t. 61, fig. 2. 1803. TYPE: *Actinea heterophylla* Juss. ≡ *Actinella* Pers., Syn. Pl. 2:469. 1807. Nom. superfl., illegit.

Based on *Actinea* Juss. ≡ Ptilepida Raf., Amer. Monthly Mag. & Crit. Rev. 2:268. 1818. Nom. superfl., illegit. Based on *Actinella* Pers. ≡ *Cephalophora* Cav. subgen. *Actinella* (Pers.) Less. Syn. Gen. Compos. 240. 1832. ≡ *Cephalophora* Cav. "sect." *Actinella* (Pers.) DC., Prodr. 5:662. 1836. Subgeneric status attributed by Candolle directly to Lessing, not intended by him as a stat. nov.

Plants perennial with one to usually several stems originating at the base, sparingly corymbosely branched above, 3 – 8 dm tall. Stems glabrous to sparsely pubescent below, becoming moderately pubescent above with short antrorse hairs. Peduncles 2 – 20 cm long, ca 1.5 – 2 times as wide at the top as at the base, moderately pubescent, becoming densely pubescent at the apex with short antrorse hairs. Leaves sparsely to moderately pubescent with short antrorse hairs, linear to linear-rhombic to narrowly elliptic to oblanceolate, entire to toothed, lobed, or pinnatifid, midrib prominent but lateral veins indistinct. Heads hemispherical to globoid, 7 – 13 mm high, 11 – 16 mm wide (excluding rays). Receptacle naked, hemispherical to globoid to ovoid, 1.5 – 3.4 mm high, 1.6 – 4.0 mm wide. Involucral bracts erect to spreading to reflexed at anthesis, in two morphologic series; the outer bracts 9 – 15, 3.8 – 7.2 mm long, 0.7 – 1.7 mm wide, free or united at the base, linear-lanceolate to lanceolate, moderately to densely pubescent with short antrorse hairs, apex acute to acuminate; inner bracts in one or two rows with ca 13 bracts in each, obovate, narrowly obovate, narrowly spatulate, narrowly rhombic, or narrowly obtrullate, 3.6 – 4.5 mm long, 0.7 – 1.6 mm wide, moderately pubescent with short antrorse hairs, apex rounded to obtuse to acute to cuspidate, the inner row of bracts, when present, essentially like the other bracts, but usually narrower. Ray florets 9 – 13, styliferous and fertile; ligules 3-lobed, 7.8 – 12.7 mm long, 2.5 – 5.5 mm wide, yellow, sparsely to densely pubescent on the undersurface with short antrorse hairs. Disc florets bisexual and fertile; disc corollas 5-lobed, cylindrical to narrowly funnelform, 3.3 – 5.7 mm long, 1.0 – 1.5 mm wide, yellow with yellow or purple lobes. Achenes 1.5 – 2.5 mm long, 0.6 – 1.2 mm wide, moderately to densely pubescent on the entire surface, but often more so on the ribs, with straight appressed hairs that are forked at the apex. Pappus scales 5 – 10, linear to linear-elliptic without a notched apex or obovate in outline with a notched apex, awned, 2.7 – 5.7 mm long including the awn, 0.7 – 1.7 mm wide, the awn 1.2 – 2.2 mm long. Chromosome numbers, $n = 17, 34$.

Distribution: Northwestern Argentina from central Prov. Salta to northwestern Prov. Córdoba, northern Prov. Mendoza, and northern Prov. San Luis; eastern Argentina from southern Prov. Corrientes to southern Prov. Buenos Aires; Uruguay.

KEY TO THE TAXA OF *HELENIUM* SECT. *ACTINEA*

1. Disc corollas with purple lobes; plants very rarely with all entire leaves, almost always at least a few leaves toothed, lobed, or pinnatifid. . . . . 1. *H. radiatum*
1. Disc corollas with yellow lobes; leaves almost always entire, rarely few-toothed.
   2. Leaves linear-rhombic, (1.1)3.5 – 6.5(10) mm wide; apex of inner involucral bracts rounded to obtuse to acute, but never cuspidate; pappus scales (5)6 – 7, obovate in outline with a notched apex, 2.7 – 3.5(4.1) mm long. . . . . 2a. *H. donianum* var. *donianum*
   2. Leaves linear, 0.9 – 2.0(2.5) mm wide; apex of inner involucral bracts acute to usually cuspidate; pappus scales 8 – 10, linear to linear-elliptic, not notched at the apex, 3.8 – 4.9 mm long. . . . . 2b. *H. donianum* var. *linearifolium*

1. HELENIUM **radiatum** (Less.) Bierner, comb. nov. BASIONYM: *Cephalophora radiata* Less. Linnaea 6:516. 1831. TYPE: URUGUAY. PROV. SORIANO or RIO NEGRO: "In Campis ad Rio Nigro," *Sellow s.n.* (LECTOTYPE: here designated the specimen labeled no. 1053 G-DC, microfiche TEX!). ≡ *Actinea radiata* (Less.) Kuntze, Rev. Gen. Pl. 1:303. 1891.

Actinea heterophylla Juss., Ann. Mus. Natl. Hist. Nat. [Paris] 2:423, t. 61, fig. 2. 1803. TYPE: URUGUAY. PROV. MONTEVIDEO: Montevideo, *Commerson herb.* 98 (HOLOTYPE: P-JU, microfiche TEX!; ISOTYPE: P-JU, microfiche TEX!). ≡ *Actinella heterophylla* (Juss.) Pers., Syn. Pl. 2:469. 1807. ≡ [*Actinea alternifolia* Sprengel, Syst. Veg. 3:574. 1826, nom. superfl.] ≡ [*Actinea heterophylla* Juss. [var.] *dentata* Kuntze, Rev. Gen. Pl. 3(3): 128. 1898, nom. superfl.] ≡ [*Actinea heterophylla* Juss. f. *bicolor* Kuntze, Rev. Gen. Pl. 3(3):128. 1898, nom. superfl.] ≡ *Cephalophora heterophylla* (Juss.) Less., Syn. Gen. Compos. 240. 1832. ≡ *Helenium heterophyllum* (Juss.) Malme, Ark. Bot. 24(6):72. 1932, non DC., Prodr. 5:667. 1836. ≡ [*Helenium mattfeldianum* Herter, Revista Sudamer. Bot. 4:206. 1937, nom. superfl.] ≡ [*Helenium alternifolium* (Sprengel) Cabrera, Revista Mus. La Plata, Secc. Bot. 4:250. 1941.]

Plants 3 – 5 dm tall. Stems sparsely pubescent below becoming moderately pubescent above. Peduncles (2)10 – 15(20) cm long, ca 2 times as wide at the top as at the base. Leaves usually moderately pubescent, narrowly elliptic to oblanceolate, entire to usually toothed, lobed or pinnatifid; plants very rarely with all entire leaves, almost always at least a few toothed, lobed or pinnatifid leaves present. Heads 7 – 11 mm high, 11 – 15 mm wide (excluding rays). Receptacle 1.6 – 2.6 mm high, 2.2 – 3.5 mm wide. Involucral bracts in two series; the outer bracts 9 – 13, united at the base, lanceolate, moderately pubescent becoming densely pubescent at the base, (3.8)4.8 – 5.9(6.9) mm long, 1.0 – 1.4 mm wide; inner bracts 10 – 13, free, narrowly obovate to narrowly rhombic to narrowly obtrullate, 3.6 – 4.5 mm long, 1.0 – 1.4 mm wide, apex acute to acuminate. Ray florets 9 – 13; ligules 9.0 – 12.0 mm long,

3.2 – 4.2 mm wide, moderately to densely pubescent on the undersurface. Disc corollas 4.4 – 5.7 mm long, 1.0 – 1.5 mm wide, yellow with purple lobes. Achenes 1.5 – 2.5 mm long, 0.6 – 1.2 mm wide. Pappus scales 8 – 9, linear to usually linear-elliptic, (3.6)4.5 – 5.7 mm long including the awn, 0.5 – 0.9 mm wide, the awn 1.2 – 1.7 mm long. Chromosome number, $n = 34$. Flowering October to April, mainly November to February. Argentina from the southern part of Prov. Corrientes to the southern part of Prov. Buenos Aires; Uruguay.

Helenium radiatum is a well-defined species that is completely allopatric to the other taxa of *Helenium*. It is relatively widespread and there is some variability in leaf shape, but there is no geographic pattern to this variability.

Problems with identification of *Helenium radiatum* often involve *Gaillardia megapotamica* (Sprengel) Baker. Morphologic similarities of their stems, leaves, ligules, disc corollas, achenes, and pappus scales are quite striking. Only two megamorphic characters, both of which are generic characteristics, consistently separate these two taxa; *Gaillardia megapotamica* has teeth-like projections on the receptacle and tapering appendages at the end of each style branch, while *Helenium radiatum* has a naked receptacle and truncate style branches.

Only $n = 34$ has been reported for this taxon (Turner et al. 1979). One count is from a population located near Concordia in Prov. Entre Rios (*Sanderson 304*, TEX), which is near the northern limit of the distribution of this species, and the other two counts are from populations near Gonzalez Chavez (*Sanderson 353*, TEX) and Coronel Dorrego (inadvertently promoted to "Gral. Dorrego" on the collection label of *Sanderson 356*, TEX) in Prov. Buenos Aires, near the southern limit of distribution. The count for *Sanderson 353* is reported as $n = 34$, but, as mentioned in Sectional Relationships, the counts for the other two are reported as $n =$ ca 34, with the voucher label for *Sanderson 356* giving the count as $n = 34II + 3I$. I believe it is significant that these counts, especially the unclear ones, are from populations separated by about 800 km. This suggests to me that polyploidy is widespread in *Helenium radiatum* and that it is probably autotetraploidy of relatively recent origin. I think it is likely, therefore, that some "ancestral" populations with $n = 17$ may still be extant and that they simply have not yet been collected and counted. It could be argued, however, that *H. radiatum* developed from tetraploid populations of *H. donianum* var. *donianum*; the latter has been reported to be dibasic with $n = 17$ and 34 (Turner et al. 1979). I think this is unlikely because the morphologic differences between the two taxa are considerable, which suggests to me that they separated at the diploid level a rather long time ago.

Chemical data also indicate that *Helenium radiatum* is a well-defined taxon. The flavonoid chemistry of *H. radiatum* is very similar to that of *H. donianum* var. *donianum* in a general sense, but it also is consistently different (Table II), and sesquiterpene lactone chemistry indicates a distinct difference between these two taxa (Herz et al. 1968; Zdero et al. 1986). Herz et al. examined three collections of *Helenium* from Argentina identified as *H. alternifolium*, an illegitimate name for *H. radiatum*. Two of their collections, however, were from near Los Puestos in Prov. Tucuman, and these plants could only be *H. donianum* var. *donianum* because this is the only taxon of *Helenium* that grows in that area. From both collections, they isolated tenulin, brevilin A, and linifolin A. Independently, Zdero et al. (1986) isolated tenulin and linifolin A, among other compounds, from one collection of *H. donianum* var. *donianum*. The other collection that Herz et al. examined was from the vicinity of La Plata in Prov. Buenos Aires, and could only be *H. radiatum*. From this collection, they isolated a new compound, alternilin; they were not able to detect any of the compounds isolated from the collections of *H. donianum* var. *donianum*.

The biology of this taxon is clearer than the nomenclature. For many years, the name *Helenium alternifolium* (Sprengel) Cabrera was used for this taxon. When Sprengel (1826) published the name *Actinea alternifolia*, however, he cited *Actinea heterophylla* as a synonym. Since there was no problem with the latter name at the time Sprengel published his substitute, the name *Actinea alternifolia* was nomenclaturally superfluous when published and, therefore, illegitimate (Article 63.1, International Code of Botanical Nomenclature, Sydney edition 1983). According to the code, only legitimate names (except homonyms) are taken into consideration for purposes of priority (Article 45.3), and a name that was illegitimate when published cannot become legitimate later unless it is conserved (Article 6.4).

Another nomenclatural problem involves the following excerpt from Kuntze (1898):

"*A. heterophylla* Juss. (*Cephalophora h.* Less., *Actinella h.* Pers., *Helenium sp.* O. Hoffm. in Engl. Pfl. - Fam.) ∝ *dentata* O. Ktze. Folia plurima dentibus paucis (2−4) magnis f. *bicolor* O. Ktze. Flores radii sulfurei albescentes, flores disci fusco-rubri. Argentina: Buenos Aires.

"β *latifolia* O. Ktze. Folia anguste lanceolata superne latiora - 4 mm lata, integerrima. Patagonia (Moreno & Tonini). Hierzu *A. radiata* Less. p. p.

"γ *linearifolia* O. Ktze. Folia linearia ± 1 mm lata integerrima. f. *concolor* O. Ktze. Flores omnes flavi. Argentina: Córdoba."

It is my opinion that Kuntze actually intended to describe only two new taxa: *Actinea heterophylla* [var.] *latifolia* and *A. heterophylla* [var.] *linearifolia*.

I believe that he named [var.] *dentata* and forma *bicolor* in the first paragraph to serve merely as the epithets at the ranks of variety and form for "typical" *Actinea heterophylla* (= *Helenium radiatum*), and thus as a means for differentiating his new taxa from it. This seems logical to me because *Helenium radiatum* typically has few-toothed leaves, yellow ligules, and purple-lobed disc corollas, and was described and illustrated as such by Jussieu (1803). In fact, I have examined three specimens (two at NY and one at US) collected by Kuntze 11 Dec 1891 in Buenos Aires that are annotated by him as "*Actinea heterophylla* Juss. var. *dentata* OK. f. *bicolor* OK.", and they are completely characteristic of *Helenium radiatum* as recognized in the present treatment. Furthermore, for Revisio Generum Plantarum vol. 3 part 2, Kuntze based his nomenclature on the Codex Nomenclaturae Botanicae Emendatus (Rev. Gen. Pl. 3(1):CCCLXXXV–CCCCXVI. 1893.) as emended in the Supplementum (Rev. Gen. Pl. 3(2):162–167. 1898). Article 32 states that a "...specific name ought, in general, to indicate something of the appearance, the characters, the origin, the history, or the properties of the species..." and Article 38 goes on to say, "Names of subspecies and varieties and mutations are formed in the same way as specific names, and are added to them according to relative value, beginning by those of the highest rank." I am certain that Kuntze followed these rules and used descriptive terms that were typical of the taxon at the ranks of variety and form rather than autonyms. By using descriptive epithets at these ranks for the typical taxon, he could use contrasting epithets for his new taxa. I have, therefore, treated *Actinea heterophylla* Juss. [var.] *dentata* Kuntze and *A. heterophylla* Juss. f. *bicolor* Kuntze as superfluous, illegitimate names.

In the second paragraph, [var.] *latifolia* is described as having absolutely entire leaves, which contrasts it with [var.] *dentata*. He does not use the rank of form because the type specimen (*Moreno & Tonini*, NY!) has yellow ligules and purple-lobed disc corollas and, therefore, is not different from the typical taxon at that rank. As it turns out, the type of *Actinea heterophylla* [var.] *latifolia* is actually a specimen of *Gaillardia megapotamica* (see excluded taxa).

In the third paragraph, the epithet *linearifolia* contrasts with *latifolia*, and the leaves are described as absolutely entire, which contrasts with typical [var.] *dentata*. In this case, Kuntze uses the rank of forma (f. *concolor*) because the plant has "flowers all yellow," which contrasts it with f. *bicolor*. It is my opinion that Kuntze was describing only one new taxon, and that again he followed his own rules and used a descriptive name, *concolor*, rather than an autonym as the epithet at the rank of forma for "typical" *A. heterophylla* [var.] *linearifolia*. The only relevant specimen that I could find

(collected by Kuntze in Dec 1891 in Córdoba and annotated by him simply as "*Actinea heterophylla* Juss. var. *linearifolia* OK.") has completely yellow ray and disc flowers. I have, therefore, treated the name *Actinea heterophylla* Juss. f. *concolor* Kuntze as superfluous and illegitimate. I agree with Kuntze that his *Actinea heterophylla* [var.] *linearifolia* is a valid taxon, but I have treated it as a variety of *Helenium donianum* rather than as a variety of *H. radiatum*.

Specimens examined: ARGENTINA: **Prov. Buenos Aires**: Buenos Aires, 11 Dec 1891, *Kuntze s.n.* (NY, US); roadside near arroyo W of Gral. [Coronel] Dorrego on rt N 3, 10 Dec 1971, *Sanderson 356* (TEX); 5 km W of Gonzales-Chavez on rt N 3, 10 Dec 1971, *Sanderson 353* (TEX); Cerro La Peregrina, 20 km N of Mar del Plata, 11 Dec 1938, *Eyerdam, Beetle & Grondona 23683* (MO)*; Sierras Pampeanas, Sierra Currumalan, Feb-Apr 1881, *Lorentz s.n.* (CORD, US); Sierra Chica, 18 Dec 1944, *Huidobro 1497* (TEX); La Ventana Mountain, Sierra de la Ventana, 13 Dec 1971, *Sanderson 363* (TEX); along Arroyo Sauce, Sierra de la Ventana, 21 Apr 1943, *Bartlett 20034* (NY); Sierra de la Ventana, 25 Nov 1944, *Huidobro 1357* (NY); Sierra de la Ventana, 27 Nov 1962, *Tell s.n.* (NY); Partido de Tornquist, Sierra de la Ventana, 22 Apr 1939, *Cabrera 5170* (US, MO); Sierra de la Ventana, Cerro Ventana, 22 Feb 1940, *Kuhnmann 24* (BA); Sierra Ventana, 1920, *Molfino s.n.* (BA); Partido Saavedra, Sierra de Curamalal, 3 Jan 1884, *Holmberg 2150* (CORD); Saldungaray, 1 Dec 1944, *Huidobro 1403* (NY); Canifrana [?], 5 Dec 1926, *Castellanos 26/1932* (BA); Partido de Olavarría, Sierras de Olavarría, Sierras Bayas, 29 Jan 1951, *Abbiatti 4026 & 4051* (US); Cerros y Laguna de Puan, 10 Nov 1928, *Scala s.n.* (US); Tandil, 2 Mar 1946, *Krapovickas 2925* (MO, US); Tandil, Las Nogales, 21 Nov 1937, *Pastore 1138* (NY); Sierra del Tandil, 12 Nov 1925, *Hosseus 222* (CORD); Sierra del Tandil, Jan 1917, *Agusti 24630* (BA); Partido Tandil, Cerro "El Sombrerito," 22 Jan 1945, *Huidobro 1768* (NY). **Prov. Corrientes**: Dept. Curuzú Cuatía, rt 14 ca km 625, 13 Dec 1957, *Pedersen 4702* US, NY). **Prov. Entre Rios**: at km 410, S of Concordia on rt N 14, 16 Oct 1971, *Sanderson 304* (TEX). URUGUAY. **Prov. Canelones**: Rio Sta. Lucia, pueblo Sta. Lucia, 21 Nov 1935, *Rosengurtt B-1374* (NY). Prov. Cerro Largo: Cerro Largo, Cerro de las Cuentas, 23 Feb 1938, *Rosengurtt B-2567* (NY). **Prov. Montevideo**: Dept. de Montevideo, Miguelete, 20 Feb 1928, *Herter 789B* (MO, NY); Carrasco, 24 Nov 1912, *Osten 6397* (US); Montevideo, Parque Lecoq, 24 Dec 1964 (US). **Prov. Rio Negro**: Dept. Rio Negro, Fray Bentos, Nov 1933, *Herter 789c* (MO). **Prov. Soriano**: Soriano, Nov 1939, *Jackson & Manzón-Heber PE-4372* (MO)*; Dept. de Soriano, km 54 between Mercedes and Cerro Verra on rt 14, 19 Jan 1977, *Irving & Irving U-24 A&B* (LL).

2. HELENIUM DONIANUM (Hook. & Arn.) Cabrera, Notas Prelim. Mus. La Plata 9:254. 1944. BASIONYM: *Cephalophora doniana* Hook. & Arn., J. Bot. (Hooker) 3:324. 1841. TYPE: ARGENTINA. PROV. MENDOZA: Mendoza, *Gillies 64* (LECTOTYPE: here designated K!). ≡ *Gaillardia doniana* (Hook. & Arn.) Grisebach, Pl. Lorenz. 140. 1874. ≡ *Actinea doniana* (Hook. & Arn.) Kuntze, Rev. Gen. Pl. 1:303. 1891.

Plants 3 – 8 dm tall. Stems glabrous to sparsely pubescent below becoming moderately pubescent above. Peduncles 7 – 20 cm long, ca 1.5 times as wide at the top as at the base. Leaves sparsely to usually moderately pubescent, linear to linear-rhombic, almost always entire, but rarely few-

toothed. Heads 10 – 13 mm high, 11 – 16 mm wide (excluding rays). Receptacle 1.5 – 2.5(3.4) mm high, (1.7)2.3 – 3.5(4.0) mm wide. Involucral bracts erect to spreading to reflexed at anthesis, in two morphologic series; the outer bracts ca 13, free or slightly united at the base, linear-lanceolate to lanceolate, moderately to densely pubescent, 4.8 – 7.2 mm long, 0.7 – 1.7 mm wide; inner bracts ca 13, often with another row of ca 13 more bracts essentially like the other inner bracts, but usually narrower, 4.0 – 4.5 mm long, 0.7 – 1.6 mm wide, from obovate to narrowly spatulate to narrowly rhombic to narrowly obtrullate, apex rounded to obtuse to acute to cuspidate. Ray florets ca 13; ligules 7.8 – 12.7 mm long, 2.5 – 5.5 mm wide, sparsely to moderately pubescent on the undersurface. Disc corollas 3.3 – 5.0 mm long, 1.0 – 1.5 mm wide, yellow with yellow lobes. Achenes 1.5 – 2.5 mm long, 0.8 – 1.0 mm wide. Pappus scales 5 – 10, linear to linear-elliptic, or obovate in outline with a notched apex, 2.7 – 4.9 mm long including the awn, 0.7 – 1.4 mm wide, the awn 1.2 – 2.2 mm long.

Helenium donianum is quite distinct from *H. radiatum* in morphology, flavonoid chemistry (Table II), and sesquiterpene lactone chemistry (see discussion under *H. radiatum*). In addition, there is good evidence for the recognition of two varieties within *H. donianum*.

Helenium donianum var. *donianum* is found mainly in the foothills of the Andes, although several specimens have been collected from the Sierras de Córdoba and the Sierras de San Luis. *Helenium donianum* var. *linearifolium* is found exclusively in Prov. Córdoba in or near the Sierras de Córdoba. The ranges of the two varieties overlap in Prov. Córdoba, but I do not know whether the taxa actually grow in the same habitat. The specimens that I have examined do not exhibit intergradation and there are no problems with identification. The leaves of var. *linearifolium* are usually distinctly narrower than those of var. *donianum*, but this distinction is not absolute. Morphologically, the pappus scales and inner involucral bracts are consistently different in the two varieties. I have recognized these taxa as varieties rather than species because the morphologic differences between them are not as great as those between *H. donianum* and *H. radiatum*.

Some systematists would argue that two taxa should be recognized within var. *donianum* because it exhibits chromosome numbers of $n = 17$ and 34 (Turner et al. 1979). It is my opinion that the evidence is insufficient to warrant such taxonomic treatment since I am unable to distinguish the $n = 17$ from the $n = 34$ plants on the basis of morphology. In addition, one count of $n = 17$ (*Turner 9203*, LL) and one of $n = 34$ (*Sanderson 374*, TEX) are from plants collected at the same locality, Cuesta de la Chilca in Prov. Catamarca.

Nomenclatural problems involved with *H. donianum* var. *linearifolium* are discussed under *H. radiatum*. The collections that I have examined, including one of my own (*Bierner 51512*, TENN), are referable to the specimen collected by Kuntze in Córdoba in 1891 (NY) and annotated by him as *Actinea heterophylla* var. *linearifolia*.

2a. HELENIUM DONIANUM (Hook. & Arn.) Cabrera var. DONIANUM

Leaves linear-rhombic, midstem leaves (3)5 − 8 cm long, (1.1)3.5 − 6.5(10.0) mm wide. Involucral bracts in two series; the outer bracts 12 − 15, 4.3 − 6.4 mm long, 0.7 − 1.4 mm wide, lanceolate to usually linear-lanceolate, apex acute to rarely acuminate; inner bracts in one or two rows with ca 13 bracts in each row, the inner row, when present, essentially like the other inner bracts, but usually narrower, 4.0 − 4.5 mm long, 0.8 − 1.2 mm wide, from narrowly obovate to narrowly obtrullate, apex rounded to obtuse to acute, but never cuspidate. Ligules 8.3 − 12.7 mm long, 2.5 − 5.5 mm wide. Pappus scales (5)6 − 7, obovate in outline with a notched apex, 2.7 − 3.5(4.1) mm long including the awn, 0.7 − 1.4 mm wide, the awn 1.2 − 1.9(2.3) mm long. Chromosome number, $n = 17, 34$. Flowering September to April, mainly December to March. Argentina from Prov. Salta to the northern part of Prov. Mendoza in the foothills of the Cordillera de Los Andes, and from the northern part of Prov. Córdoba to the northern part of Prov. San Luis in the Sierras de Córdoba and the Sierras de San Luis.

Specimens examined: ARGENTINA. **Prov. Catamarca**: Cuesta de la Chilca, NE of Andalgalá, Feb 1974, *Turner 9203* (LL); top of Cuesta de la Chilca on rt N 62, E of Andalgalá, 17 Dec 1971, *Sanderson 374* (TEX); Dept. Capital, Las Carreras [Barreras?], 23 Apr 1928, *Venturi 6269* (US); Dept. Andalgalá, Común El Sancho [Funda?], 20 Dec 1896, *Jorgensen 1663* (MO, US); Rió de las Granadillas, cerca Belen, Dec 1879, *Schickendantz 46* (CORD); Quebrada del Carrizal, Feb 1876, *Schickendantz 248* (CORD); Loma Cruzada (S Ambato), Feb 1941, *Parodi 14292* (US); Agua Negra, 9 Feb 1930, *Castellanos 30/681* (BA); Quebrada de La Sevila, ca 10 km SE of jct of rt 1 and rt 60 along rt 60, 10 Feb 1973, *Dillon & Rodriguez 526* (LL); Dept. Tinagasta, Cuesta de Zapata, 2 Mar 1967, *Cabrera et al. 18109* (TEX). **Prov. Córdoba**: Capilla del Monte, 28 Jan 1922, *Castellanos 24625* (BA); Dept. Punilla, Capilla del Monte, 1894, *Doering 8253* (CORD); Dept. Cruz del Eje, Cruz del Eje, Ojo de Agua, 29 Jan 1885, *Kurtz 247 & 254* (CORD); Gutemberg (km 288, Ferrocarril Central de Argentina), 24 Mar 1943, *Bartlett 19807* (US). **Prov La Riója**: km 1133 on rt 60, 90 km N & W of La Riója, 31 Dec 1974, *Bacon & Bohnstedt 1529* (LL); Velazco, Puerto Viejo, Jan 1934, *Yepes {?} 18890* (BA); Dept. Gral. Sarmiento, Punta de Agua, Precordillera, 31 Jan 1947, *Hunziker 2084* (BA); Dept. Famatina, Las Gredas, 26 Feb 1965, *Cabrera et al. 16702* (TEX); Dept. Famatina, La Mariposa, Sierra Famatina, 31 Jan 1906, *Kurtz 13386* (CORD); Dept. Famatina, Sierra Famatina, La Vega de La Hoyada, 22 Jan 1908, *Jimenez 15198* (CORD); Dept. Famatina, Mina San Juan, 2 Mar 1906, *Kurtz 13672* (CORD); Dept. Gral. Lavalle, Sierra de Sañogasta entre Guálo y Puesto Talampayo, 27 Jan 1906, *Kurtz 13294* (CORD); Dept. Sanagasta, Sierra Velasco, Cuesta de La Casa de

Piedra, 28 Feb 1908, *Kurtz 15458* (CORD); Las Cortaderas entre el Peñon y el Faguel [?], Cordillera de la Riója, 22 Feb 1879, *Hieronymus & Niederlein 203* (CORD). **Prov. Mendoza**: Dept. Las Heras, Las Chilcas, 17 Jan 1897, *Kurtz 9294* (CORD); Dept. San Carlos, 30 leguas al sur de Mendoza, 19 – 27 Feb 1885, *Loos 2377* (CORD); Villavicencio, N of Mendoza, 5 Jan 1936, *Mexia 4399* (MO, US). **Prov. Salta**: Dept. Rosario de la Frontera, ca 6 km SW of Rosario de la Frontera on hwy 55, 15 Jan 1975, *Bacon & Bohnstedt 1628* (LL); Dept. La Candelaria, Menguillo [Unguillo?], Sierra Colorada, Jan 1933, *Schreiter 9412* (US)*; Dept. Capital, Salta, 5 Mar 1958, *Cabrera & Marchionni 12.807* (US)*. **Prov. San Juan**: Dept. Calingasta, Llanos de Leoncito del Norte, Mina El Molle, 28 Jan 1950, *Castellanos 15.333* (US); Dept. Iglesia, Gds. [?] del Molle, al N de Malimán, NE del Colanguil, 27 Feb 1950, *Perrone 55.249* (BA); Bajada de la Cuesta Vieja, 28 Feb 1921, *Hosseus 2594* (CORD); Valle del Rió de Los Chupadores, 28 Feb 1921, *Hosseus 2538* (CORD). **Prov. San Luis**: Dept. Junín, Bajo de los Velez [?], 19 Feb 1942, *Maldonado 1284* (US)*. **Prov. Tucumán**: Dept. Burroyacu, El Puestito, 20 Sep 1928, *Venturi 7327* (MO, US)*; Dept. Capital, Rió Talí [?], 19 Nov 1920, *Venturi 1050* (US)*; Dept. Cruz Alta, Estación Aráoz, 21 Nov 1925, *Schreiter 3993* (US); Dept. Cruz Alta, Canipe [Campo?] Alegre, km 754 E.C.C.N., 29 Oct. 1922, *Venturi 1999* (US); Tapia, 23 Nov. 1920, *Venturi 1070* (US)*; Trancas, 14 Dec 1912, *Rodriguez 1189* (NY); Tucumán, Oct. 1892, *Kuntze s.n.* (NY, US).

2b. Helenium donianum (Hook. & Arn.) Cabrera var. **linearifolium** (O. Kuntze) Bierner, comb. nov. Basionym: *Actinea heterophylla* Juss. [var.] *linearifolia* Kuntze, Rev. Gen. Pl. 3(3):128. 1898. Type: ARGENTINA. Prov. Córdoba: Córdoba, Dec 1891, *Kuntze s.n.* (lectotype: here designated NY!). ≡ [*Actinea heterophylla* Juss. f. *concolor* Kuntze, Rev. Gen. Pl. 3(3):128. 1898, nom. superfl.]

Leaves linear, midstem leaves 2 – 5(6) cm long, 0.9 – 2.0(2.5) mm wide. Involucral bracts in two series; the outer bracts usually 13, lanceolate, acuminate, 5.0 – 7.2 mm long, 1.4 – 1.7 mm wide; inner bracts usually 13, obovate to narrowly obovate, acute to usually cuspidate, 4.1 – 4.4 mm long, 0.7 – 1.6 mm wide. Ligules 7.8 – 10.0 mm long, 2.9 – 4.0 mm wide. Pappus scales 8 – 10, linear to linear-elliptic, the body not notched at the apex, 3.8 – 4.9 mm long including the awn, 0.7 – 1.0 mm wide, the awn 1.7 – 2.2 mm long. Flowering November to February. Argentina, Prov. Córdoba in the Sierras de Córdoba and nearby lower elevations.

Specimens examined: ARGENTINA. **Prov. Córdoba**: Córdoba, Dec 1891, *Kuntze s.n.* (NY); Córdoba, 23 Dec 1975, *Bierner 51512* (TENN); Córdoba, 19 Nov 1880, *Galander s.n.* (CORD); San Javier, 30 Nov 1927, *Castellano 11830* (BA); Dept. Santa María, La Isla, 11 Dec 1950, *A. de la Sota 3106* (US); cerca del Matadero, Sierra Achala de Córdoba, 2 Dec 1878, *Hieronymus s.n.* (CORD); Dept. Punilla, entre Durazno y Cerro Blanco (arriba de Tanticuchi), 18 – 20 Feb 1911, *Flossdorf 15965* (CORD).

SYNONYMY FOR EXCLUDED NAMES AND TAXA (SOUTH AMERICA)

HYMENOXYS ANTHEMOIDES (Juss.) Cass., Dict. Sci. Nat. 55:278. 1828.

BASIONYM: *Hymenopappus anthemoides* Juss., Ann. Mus. Natl. Hist. Nat. [Paris] 2:426. 1803. TYPE: ARGENTINA. PROV. BUENOS AIRES: Buenos Aires, 1767, *Commerson s.n.* (HOLOTYPE: P-JU; ISOTYPE: P-JU). See Parker (1962). ≡ *Actinella anthemoides* (Juss.) A. Gray, Proc. Amer. Acad. Arts 13:373. 1878. ≡ *Actinea anthemodes* (Juss.) Kuntze, Rev. Gen. Pl. 3(3):128. 1898. Orthographic variant. ≡ *Actinella anthemidoides* (Juss.) Malme, Ark. Bot. 24(6):73. 1932. Orthographic variant. ≡ [*Actinella anthemoides* (Cass.) Herter, Revista Sudamer. Bot. 4:206. 1937, nom. superfl.]

Actinea haenkeana (DC.) Kuntze, Rev. Gen. Pl. 3(3):128. 1898. BASIONYM: *Hymenoxys haenkeana* DC., Prodr. 5:661. 1836. TYPE: PERU. 1790, *Haenke s.n.* (HOLOTYPE: G-DC; ISOTYPE: P). Parker (1962) believes that these plants were actually collected in Argentina.

HYMENOXYS TWEEDIEI Hook. & Arn., J. Bot. (Hooker) 3:323. 1841.

TYPE: BRAZIL. "Rio Grande, and dry pastures, roadsides of Los Loamos, N. Patagonia," *Tweedie 859* (HOLOTYPE: K). See Parker (1962). ≡ *Actinea tweedii* (Hook. & Arn.) Kuntze, Rev. Gen. Pl. 3(3):128. 1898. Orthographic variant. ≡ *Actinella tweediei* (Hook. & Arn.) Malme, Ark. Bot. 24(6):73. 1932.

GAILLARDIA MEGAPOTAMICA (Sprengel) Baker in Mart., Fl. Bras. 6(3):276. 1884. BASIONYM: *Guntheria megapotamica* Sprengel, Syst. Veg. 3:449. 1826. TYPE: BRAZIL. "Rio grande," Sello[w] (HOLOTYPE: P).

Actinea heterophylla Juss. [var.] *latifolia* Kuntze, Rev. Gen. Pl. 3(3):128. 1898. TYPE: ARGENTINA. Patagonia, *Moreno & Tonini s.n.* (NY!).

BLAINVILLEA BAHIENSIS (DC.) Baker in Mart., Fl. Bras. 6(3):177. 1884.

BASIONYM: *Oligogyne bahiensis* DC., Prodr. 5:629. 1836. TYPE: BRAZIL. "circa Bahiam Brasiliae," *Blanchet 1706* (HOLOTYPE: G-DC).

Galophthalmum brasiliense Nees et Mart., Nova Acta Leop. 12:8, t. 2. 1824. Type not seen; taxonomic synonym of *Blainvillea bahiensis* according to Gray Index. ≡ [*Actinea oppositifolia* Sprengel, Syst. Veg. 3:574. 1826, nom. superfl.]

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APPENDIX

Voucher specimens for sect. *Actinea* are indicated by asterisks in the lists of specimens examined. The following voucher specimens for sect. *Cephalophora* are deposited in the University of Tennessee Herbarium (TENN), and all collection numbers are those of M. W. Bierner. *Helenium aromaticum*—CHILE. Aconcagua: 27.0 km S of the Aconcagua—Coquimbo Prov. line on hwy 5, *51452*. Coquimbo: 13.7 km N of the Coquimbo—Aconcagua Prov. line on hwy 5, *51454;* 16.6 and 6.5 km S of turnoff to Cta. Huentelauquen on hwy 5, *51455 and 51456;* 57.3 km S. of Ba. El Teniente on hwy 5, *51459;* 2.0 km S of turnoff to Comunidad Herradura on hwy 5, *51464;* Just S of Guayacan and Coquimbo at km 453.4 on hwy 5, *51469;* Dirt rd 0.6 km E of Las Rojas in the Elqui Valley E of La Serana, *51472*. Valpariso: 8.8 km W of hwy 5 on rd from Nogales to Puchuncavi, *51451*. *Helenium atacamense*—CHILE. Atacama: S of Vallenar on hwy 5 at km 649.6, 656.5, and 653.3, *51489, 51493 and 51494;* N of Vallenar on hwy 5 at km 673.3 and 673.6, *51490 and 51492*. *Helenium urmenetae* var. *leguiffei*—CHILE. Coquimbo: Dirt rd 2.5, 3.4, and 4.2 km W of Las Rojas in the Elqui Valley E of La Serana, *51476, 51478 and 51479;* Hwy 5, 8.5 km S, 0.4 km N, and 25.0 km N of the entrance to El Tofo mine, *51482, 51484 and 51485*. *Helenium vallenariense*—CHILE. Atacama: hwy 5, 32.6 and 50.3 km N of the Atacama—Coquimbo Prov. line at km 620.9 and 638.7, *51488 and 51495*. Coquimbo: Hwy 5, 3.4 and 0.9 km S of the Coquimbo—Atacama Prov. line, *51486 and 51487*.

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A NEW *VITIS* (VITACEAE) FROM VERACRUZ, MÉXICO

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ABSTRACT

Vitis **nesbittiana**, a new species in series *Aestivales* Planchon (Vitaceae), is described and compared with two morphologically similar members of *Aestivales*. *Vitis* **nesbittiana** is restricted to tropical cloud forests around Jalapa, México at elevations from 1700 – 2120 m.

A new species of grapes with conspicuously glaucous abaxial leaf surfaces was found growing on hillsides in tropical cloud forests near Jalapa, Veracruz, México. This species belongs in series *Aestivales* Planchon (Vitaceae), a series formerly restricted to the United States east of the Rocky Mountains. Series *Aestivales* is unique in the occurrence of glaucescent to glaucous abaxial leaf surfaces and reddish – brown wood on one year old stems, which also may be glaucous, especially around nodes. This series formerly consisted of a single species, *V. aestivalis* Michx., which occurs as regional variants that have non – overlapping distributions, freely intergrade, occupy relatively xeric, often sandy sites, and flower before sympatric members of series *Cinerascentes*. *Vitis aestivalis* consists of five subspecific taxa: var. *aestivalis* (including *V. gigas* Fennell and *V. rufotomentosa* Small), var. *argentifolia* (Munson) Fernald, var. *glauca* Bailey (= *V. lincecumii* var. *glauca* Munson), var. *lincecumii* (Buckley) Munson, and var. *smalliana* (Bailey) Comeaux.

This species is dedicated to the memory of Dr. William B. Nesbitt (1932 – 1983), former grape breeder at North Carolina State University. Dr. Nesbitt developed numerous cultivars of grapes and served as chairman of the author's advisory committee for the doctorate degree during the research period.

VITIS **nesbittiana** Comeaux, sp. nov. Fig. 1, 2.

Caules angulatescens teres, canus ad bruno, striae obscuri ad basim; folia magni, saepe trilobi, laterilobis acutatis ad acuminatis et divergentibus, *lobus terminalis acuminatus, basibus cordata ad fere truncata*, abaxialis pagina glauca, glabrata ad obscura puberula; baccae niger, glaucae, 7 – 15 mm diam.; semina 3.5 – 7 mm longa, 3 – 5 mm lata, rostro brevi, *dorsalis pagina saepe ferens 2 – 6 sulcati perpendiculares ad verticalis axis*.

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Large vine to 20 m. Stems on current season growth glabrous to flocculent, occasionally glaucescent; branchlets angled becoming terete and obscurely striate, internodes 3 – 12 cm long, nodes not encircled with red pigmentation, pith interrupted at nodes by a diaphram 2 – 3 mm thick; one year old stems extremely flexible; bark gray to brown (not reddish brown) and shredding on one year old stems, lenticels absent; growing tips glabrescent and red to pubescent with tan to rufescent trichomes, not enveloped by young leaves; bud scales glabrous to puberulent, 3 – 5 mm long, brown. Leaves cordiform to nearly deltoid, rugose to flat, apex acuminate to nearly acute, base cordate to nearly truncate, margins almost entire to serrate, with teeth 0.1 to 7 mm long, oriented perpendicular to margin or towards apex, convex or triangular, occasionally ciliate, with veins extending beyond teeth or margin, lateral lobes acute to acuminate, then divergent, lateral sinuses mostly acute; lamina with glabrous adaxial surfaces on mature leaves, abaxial surfaces distinctly glaucous, usually glabrous or sometimes puberulent on mature leaves, with or without tufts of trichomes in axils of major veins, 9 – 20 cm wide, 13 – 25 cm long, petioles glabrous to floccose, 5 – 13 cm long; stipules brown, pubescent, 1 – 1.5 mm long, 1 – 1.5 mm wide, caducous; pubescence white, tan or rufescent, consisting of straight, pointed, simple trichomes or arachnose trichomes. Tendrils and inflorescences absent every third node, tendrils bifurcate or trifurcate, to 17.5 cm long. Inflorescences 2 – 9.5 cm long, peduncles 1.5 – 3.2 cm long, shoulder 1 – 5 cm long, occasionally replaced by a tendril. Flowers not observed. Fruit a berry, black, glaucous, without lenticels, subovate to spherical, 0.7 – 1.5 cm in diameter, with a pleasant vinous flavor when fully ripened; skin thin; pulp clear, greenish to purplish, melting; juice clear to purplish. Seeds tan to brown, irregular in shape, ovate to nearly pyriform, 3.5 – 6 mm long, 3 – 4.5 mm wide, generally with 2 – 6 shallow grooves on the dorsal surface arranged perpendicular to the vertical axis.

TYPE: MÉXICO. 18 km W jct Hwy 140 and Ave. Americans in Jalapa, 2110 m elev., 8 Sep 1986, *Comeaux 4138* (HOLOTYPE: SMU; ISOTYPES: MEXU, PH)

PARATYPES: MEXICO. VERACRUZ: 20.5 km W jct Hwy 140 and Ave. Americans in Jalapa, 2120 m elev., 23 Jun 1986, *Comeaux 4134* (SMU); 20 km l.c., 23 Jun 1986, *Comeaux 4135* (SMU); 19.5 km l.c., Jun 1986, *Comeaux 4136* (SMU); 18 km l.c., 23 Jun 1986, *Comeaux 4137* (SMU); 15 km l.c., 23 Jun 1986, *Comeaux 4139* (SMU); 12 km SW of La Reforma, 1760 m elev., 23 Jun 1986, *Comeaux 4169* (SMU); 18 km l.c., 23 Jun 1986, *Comeaux 4171* (SMU); 45.6 km l.c., 2030 m elev., 23 Jun 1986, *Comeaux 4172* (SMU).

Field studies revealed *V. nesbittiana* to be endemic to a restricted area including Jalapa, Veracruz north 20 km and west 20 km. Terrain is mountainous, 1700 to 2120 m elevation, and within cloud forests. *Vitis*

nesbittiana was not found in similar cloud forests north of Jalapa near Cuidad Valles or south of Jalapa at Huatusco. Associated species of *Vitis* included *V. popenoii* Fennell and *V. tiliifolia* Humb. & Bonpl. ex Roem. & Schult.

The glaucous, mostly glabrous abaxial leaf surfaces of *V. nesbittiana* are suggestive of *V. aestivalis* var. *argentifolia* (Munson) Fernald and *V. aestivalis* var. *glauca* Bailey. Leaves of *V. nesbittiana* generally are more acuminate and have broader basal sinuses, occasionally appearing nearly truncate. One year old stems of *V. nesbittiana* vary from gray to brown, and lack the reddish – brown appearance that is characteristic of series *Aestivales* in the United States. Also, the one year old stems of *V. nesbittiana* are unique in being flexible, unlike the relatively brittle wood of other *Aestivales*.

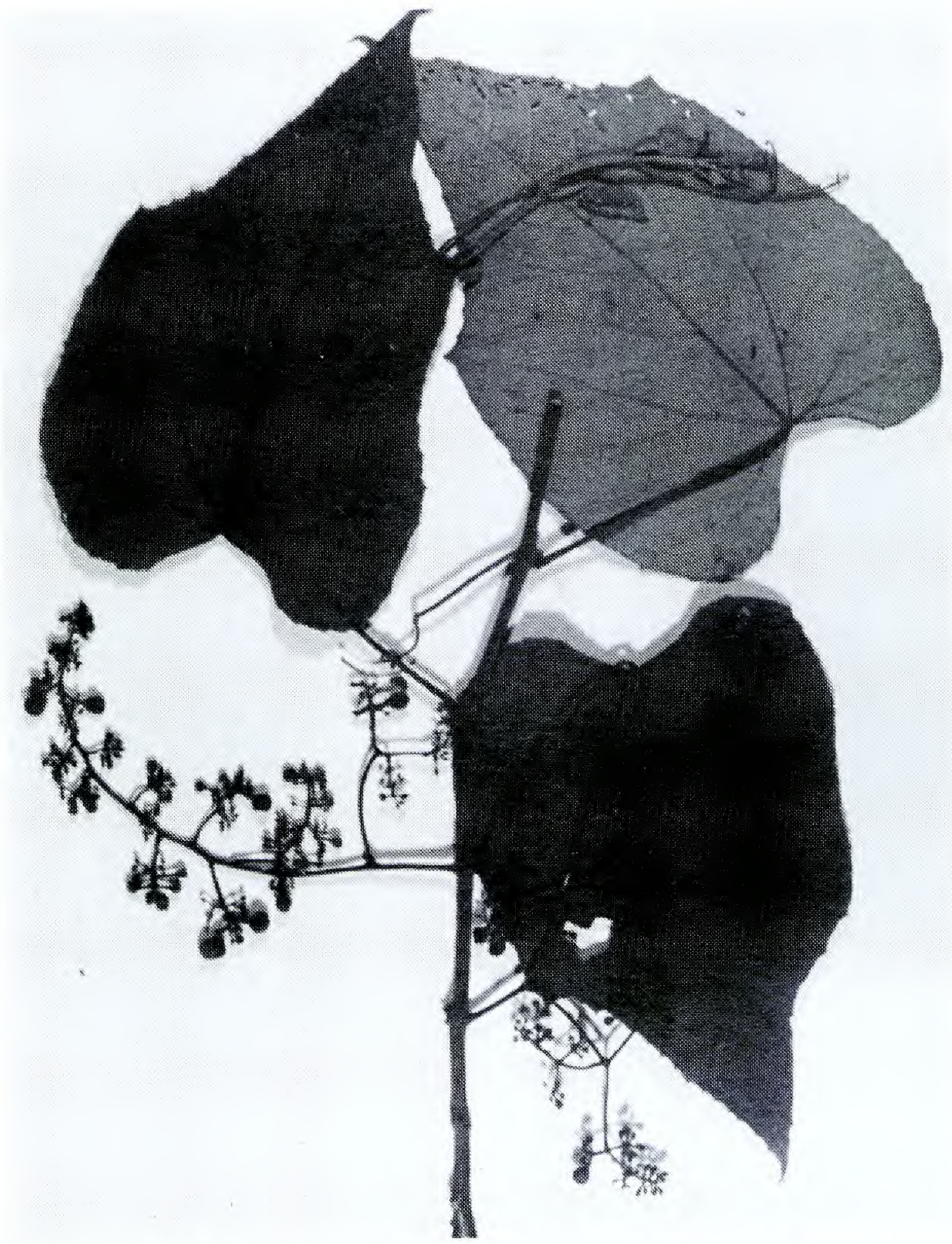

FIG. 1. Type specimen of *Vitis nesbittiana* (*Comeaux 4138*).

FIG. 2. *Vitis nesbittiana (Comeaux 4138).* a) habit, b) inflorescence with mature fruit, c) seed, dorsal surface (left) and ventral surface (right).

TABLE 1. Berry diameters and seed number for *Vitis nesbittiana*, *V. aestivalis* var. *argentifolia*, and var. *glauca*.

	Diameter in cm for 10 berries from each vine											
	Berries with 1 seed			Berries with 2 seeds			Berries with 3 seeds			Berries with 4 seeds		
SPECIES	×	RANGE	n	×	RANGE	n	×	RANGE	n	×	RANGE	n
1												
V. nesbittiana	1.0	0.7 – 1.2	15	1.1	1.0 – 1.2	8	1.2	1.0 – 1.5	5	1.4	1.4 – 1,4	2
2												
V. a. var. *glauca*	1.1	0.8 – 1.3	34	1.2	0.9 – 1.4	32	1.3	1.0 – 1.5	20	1.3	1.1 – 1.5	14
3												
V. a. var. *argentifolia*	0.8	0.6 – 1.1	50	1.0	0.7 – 1.2	43	1.0	0.8 – 1.3	52	1.1	0.9 – 1.5	44

× = mean, n = observations

1 = 3 vines sampled, 2 = 10 vines sampled, 3 = 19 vines sampled (1 berry with 5 seeds not included above)

TABLE 2. Seed characteristics in mm for *Vitis nesbittiana*, *V. aestivalis* var. *argentifolia*, and var. *glauca* (n = 10).

		Seed Length/Width		Seed Index[1]		Rostrum	
SPECIES	Number of Samples	Mean	Range	Mean	Range	Mean	Range
V. nesbittiana	3	5.1/4.2	3.5 – 6.0/ 3.0 – 4.5	0.83	0.73 – 1.0	0.72	0.1 – 1.0
V. a. var. *glauca*	10	5.9/4.2	4.0 – 7.0/ 3.5 – 5.0	0.71	0.62 – 0.90	1.2	0.5 – 2.5
V. a. var. *argentifolia*	10	5.0/3.9	3.5 – 7.0/ 3.5 – 5.0	0.78	0.64 – 1.0	0.75	0.1 – 1.0

[1]Seed Index = seed width divided by length

Vitis nesbittiana is distinguished from *V. aestivalis* by fruit and seed characters (Tables 1 & 2). Fruit of *V. nesbittiana* are generally larger than *V. aestivalis* var. *argentifolia* and similar in size to *V. aestivalis* var *glauca*. Conversely, seeds of *V. nesbittiana* and *V. aestivalis* var. *argentifolia* have similar sizes, whereas seed of *V. aestivalis* var. *glauca* are larger. Seeds of *V. nesbittiana* are unique among subgenus *Vitis* in North America in normally having 2 – 6 shallow grooves on the dorsal surface arranged perpendicular to the vertical axis.

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Beltsville Symposium XIII

BIOTIC DIVERSITY AND GERMPLASM PRESERVATION—GLOBAL IMPERATIVES

May 9 – 11, 1988

Beltsville Agricultural Research Center, Beltsville, Maryland

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NOMENCLATURAL CLARIFICATION OF THE NAME *VITIS SIMPSONII* MUNSON (VITACEAE)[1]

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ABSTRACT

The name *Vitis simpsonii* Munson has been applied by Munson and other authors to two different taxa. This has resulted in nomenclatural confusion in attempts to characterize and classify these taxa. *Vitis simpsonii* Munson of 1887 is treated in synonomy under *Vitis cinerea* Engelm. ex Millard. var. *floridana* Munson of series *Cinerascentes*. *Vitis simpsonii* Munson of 1890 is synonomized under *Vitis aestivalis* Michaux var. *smalliana* (Bailey) Comeaux of series *Aestivales*.

INTRODUCTION

The name *Vitis simpsonii* Munson historically has been applied in the literature to two distinct taxa found in the southeastern United States. Munson had been sent grapes from Florida by J. H. Simpson on different dates. Munson (1887) named one *Vitis simpsonii* in honor of J. H. Simpson. However, Munson (1890) reduced this taxon to varietal rank under *V. cinerea*. To retain an honor to Simpson, he then named a second grape *Vitis simpsonii* (Munson, 1890). Therefore, Munson described two distinct grape taxa with the same name. Taxonomists historically have been confused on the application of the name *Vitis simpsonii* as a result.

The nomenclatural confusion is compounded by a third grape sent by Simpson and originally labeled questionably as *Vitis caribaea* DC. These grapes will be listed as taxa numbers one to three in this paper to guide the reader through the complicated nomenclatural history.

NOMENCLATURAL HISTORY

Table 1 provides an overview of the major taxonomic publications relating to the taxa involved. Munson (1887) published a listing of native

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American grapes with a phenological table. Two grapes obtained from Florida and sent to Munson by J. H. Simpson are cited in the list. Both were accompanied by a footnote.

Taxon number one was cited as *Vitis simpsonii*, named in honor of its discoverer, J. H. Simpson. Taxon number two was cited as *Vitis caribaea* (?) DC. and referred to as the Prof. Curtiss' grape. A footnote accompanying taxon number one indicated that Munson apparently was not certain of the status of Prof. Curtiss' grape, alluding to the possibility that these two grapes might be of the same species.

Munson (1890) created confusion regarding the name *Vitis simpsonii* by two distinct actions. It is apparent now that Munson (1890) concluded that Taxon number one was a variety of *V. cinerea* which he named var. *floridana* Munson. This conclusion becomes evident because Munson (1890) did not cite *V. simpsonii* Munson of 1887 in synonymy until later (Munson 1909).

The second action involved another grape (Taxon number three) sent to Munson from Florida by J. H. Simpson. Munson (1890) placed it in series *Aestivales* and gave it the name *Vitis simpsonii*. Munson (1909) described it as having deeply lobed leaves and large glaucous fruits, unlike the description of small fruits of the grape of 1887. Therefore, there became two distinct grape taxa of different series that historically have borne the name

TABLE 1. Nomenclatural interpretation of three taxa associated with the name *Vitis simpsonii* Munson.

TAXON[1]	**Munson** 1887	**Munson** 1890/1909	**Small** 1903	**Bailey** 1934	**Fernald** 1936	**Rogers & Mortensen** 1979
Taxon One	*V. simpsonii* Munson, sp. nov.	*V. cinerea* var. *floridana* Munson (1890)	*V. austrina* Small, sp. nov.	*V. simpsonii* Munson	*V. cinerea* var. *floridana* Munson	*V. aestivalis* ssp. *divergens* Rogers nom. inval. *V. aestivalis* ssp. *simpsonii* (Bailey) Rogers
Taxon Two	*V. caribaea* (?) DC. "Prof. Curtiss grape"	*V. caribaea* DC. (1890) *V. cinerea* × *V. simpsonii* (1909)		*V. sola* Bailey, sp. nov.		*V. aestivalis* ssp. *sola* (Bailey) Rogers
Taxon Three	*V. simpsonii* Munson (1890) sp. nov. (nom. superfl.)	*V. simpsonii* Munson (1890, not 1887)		*V. smalliana* Bailey, sp. nov.		*V. aestivalis* ssp. *smalliana* (Bailey) Rogers

[1]Comeaux & Fantz recognize Taxon One and Taxon Two in this paper as *Vitis cinerea* var. *floridana* and Taxon Three as *Vitis aestivalis* var. *smalliana*.

Vitis simpsonii. Munson's action is the source of present nomenclatural problems with the name *Vitis simpsonii* Munson.

These taxonomic publications by Munson provide the foundation for our nomenclatural history. We will now follow each taxon separately to minimize confusion.

Nomenclatural history of taxon one.

Munson (1890) had recognized this grape as *Vitis cinerea* var. *floridana* Munson. The name *V. simpsonii* Munson of 1887 is therefore a synonym.

Small (1903) disagreed with Munson's conclusions that this grape was a variety of *V. cinerea*. He recognized it as a distinct species, naming it *V. austrina* Small. The name *V. cinerea* var. *floridana* was cited in synonymy.

Small also cited the name *V. simpsonii* Munson as a distinct species. The description by Small is obviously that of taxon number three, the *V. simpsonii* Munson of 1890, not of taxon number one, the *V. simpsonii* Munson of 1887.

Small (1933) cited *V. simpsonii* Munson and *V. cinerea* in his manual for plants of the Southeastern United States. He does not include *V. austrina* or *V. cinerea* var. *floridana*. Small described *V. cinerea* as pubescent, with ashy or dark brown trichomes.

Bailey (1934) disagreed with Munson's conclusions of 1890 that taxon number one was a variety of *V. cinerea*. Bailey considered it a distinct species, placing it in series *Aestivales* and recognized it as *V. simpsonii* Munson (1887).

Fernald (1936) defended Munson's treatment of this taxon as *V. cinerea* var. *floridana*. However, he unfortunately contributed to the nomenclatural confusion in *Vitis* at the same time by incorrectly citing in synonymy *V. simpsonii* Munson of Small (1933). This error had been made earlier by Hedrick (1908) and repeated by Gleason and Cronquist (1963).

Rogers and Mortensen (1979) recognized this taxon as a subspecies of *V. aestivales*, naming it *V. aestivalis* ssp. *simpsonii* (Munson) Rogers. Evidence comes from Roger's annotation of specimens of *V. cinerea* var. *floridana*. These included a syntype (24 April 1890, *Munson s.n.*, BH!) plus other collections (1 June 1896, *Munson s.n.*, MO!; *Tracy* 7478, MO!; *Godfrey et al. 63512*, FSU!). Their interpretation of subspecies *simpsonii* also included, however, some members of series *Aestivales*. For example, the vine labeled *V. aestivalis* ssp. *simpsonii* that was used as the parent plant in developing Lake Emerald is actually 'Pixiola' (Stover 1954). 'Pixiola' is a selection from native Floridian grapes bearing unusual green-colored fruit when ripe. Examination by the senior author of living specimens of 'Pixiola' at the University of Florida, Agricultural Research Center,

Leesburg, revealed that 'Pixiola' produced only three lobed leaves with glaucous abaxial surfaces. Thus it is *V. aestivalis* var. *aestivalis*.

Rogers and Mortensen (1979) placed the name *V. rufotomentosa* Small in synonymy with *V. aestivalis* ssp. *simpsonii*, a taxon earlier considered synonymous by Fernald (1939) with *V. araneosa* LeConte. Examination by Comeaux of the types of *V. araneosa* (*LeConte s.n.*, PH 850609-11!) and *V. rufotomentosa* (*Nash* 525, NY!) revealed glaucous abaxial leaf surfaces. Therefore, these types are members of *V. aestivalis* var. *aestivalis*.

Rogers and Mortensen (1979) described *V. aestivalis* ssp. *divergens* Rogers as leaves frequently with divergent lobes, large lax inflorescences with angled axes, small seeds, and frequent occurrence in lowlands. These characteristics are consistent with taxon one. This name has not been validly published, since Rogers did not provide a Latin diagnosis or designation of type specimens.

Nomenclatural history of taxon two.

Munson (1890) cited *Vitis caribaea* as occurring only in the West Indies and eastern Mexico. Therefore, Munson implied indirectly that he had not accepted this name for taxon two in his publications of 1887. Munson (1909) continued to dispute the occurrence of *V. caribaea* in the United States and concluded that the specimens sent to him by Prof. Curtiss were likely to be hybrids of *V. simpsoniii* (of 1890) and *V. cinerea*.

Bailey (1934), in his taxonomic treatment of North American *Vitis*, named Prof. Curtiss' grape (taxon number two) *V. sola* Bailey. He concluded that this taxon was unlike the tropical *V. caribaea*, and therefore concurred with Munson (1909). However, Bailey treated it as a distinct species, and not a hybrid as Munson (1909) implied. *Vitis sola* was described as having broad leaves with margins continuous or sinuate, with each vein extending beyond the margin. The cited holotype was *Curtiss 4791* (BH!), originally labeled as *V. caribaea* by Bailey (1897). Bailey (1934) cited *Curtiss 4747* (MO!) and *6415* (MO!) which are paratypes according to the international code.

Rogers and Mortensen (1979) concluded that this grape taxon was a subspecies of *Vitis aestivalis*. Therefore, they adopted the name *V. aestivalis* ssp. *sola* (Bailey) Rogers. The glaucous abaxial leaf surfaces of this taxon of Rogers in cultivation at North Carolina State University (*Rogers 654*) and collections of *V. aestivalis* (*Godfrey 71154*, FSU!; *Curtiss 4747*, MO!) annotated by Rogers as *V. aestivalis* ssp. *sola* indicate that members of series *Aestivales* were considered as part of this taxon. Other annotations by Rogers of *V. aestivales* ssp. *sola* (*Curtiss 6415*, GH!; *Wiggins 19841*, USF!) are *V. cinerea* var. *floridana*. As a final note on *V. caribaea*, Bailey (1934)

followed Urban (1907) in placing this name in synonymy with *V. tiliifolia* Humb. & Bonpl. ex Roem. & Schult due to nomenclatural priority. Elias (1968) accepted this treatment and excluded the U.S. from its distribution.

Nomenclatural history of taxon three.

Munson (1890) incorrectly utilized the name *Vitis simpsonii* Munson for this taxon, as he used the same name three years earlier for a different taxon with conspicuously smaller fruits. As a later homonym, this name is an illegitimate name according to the international rules of botanical nomenclature.

Small (1903, 1933) cited *V. simpsonii* Munson in his flora and manual for plants of the Southeastern United States. The description by Small is obviously that of taxon number three, the *V. simpsonii* Munson of 1890, not 1887.

Bailey (1934) recognized that *V. simpsonii* as applied to this taxon was a later homonym and contrary to the international rules of nomenclature. Therefore, he proposed the name *V. smalliana* Bailey.

Rogers and Mortensen (1979) concluded that taxon three was a subspecies of *V. aestivalis*. They proposed the name ssp. *smalliana* (Bailey) Rogers.

DISCUSSION AND CONCLUSIONS

Both taxa named *Vitis simpsonii* bear variously lobed leaves, with some individuals of taxon number one producing lobed and unlobed leaves (Comeaux et al. 1987; Munson 1909). Lobed versus unlobed leaves was a characteristic used by earlier taxonomists in differentiating species of grapes (Bailey 1934; Rogers and Mortensen 1979) and resulted in inaccurated concepts of the species.

Taxa numbers one and two.

Morphological variation in these taxa has resulted in misapplication and confusion in names. We agree with Munson (1890) and Fernald (1936) in the recognition of the name *Vitis cinerea* var. *floridana* Munson for taxon number one. We disagree with the conclusions of Small (1903) and Bailey (1934) that it is a distinct species. If it were a distinct species, Bailey (1934) would be correct in application of the name *V. simpsonii* Munson whereas the name *V. austrina* Small would be superfluous. The angled stems, branches, and axes of inflorescences, plus the absence of glaucousness on abaxial leaf surfaces, a preference for moist sites, and a later flowering period indicate taxon one is a relative of *V. cinerea* (series *Cinerascentes*).

TABLE 2. Characteristics of selected specimens examined from complexes associated with *Vitis simpsonii*.

SPECIMEN	STEMS					TENDRILS		LEAVES								
	STEMS ANGLED	STEMS STRIATED	STEMS PUBESCENT	Growing tip	Trichome color	PATTERN	SEQUENCE	STIPULE LENGTH (MM)	PETIOLE PUBESCENCE	GLAUCOUSNESS	LOBES	Teeth size	Upper surface pubescent	Lower surface pubescent	Midrib pubescence	Axillary tufts
V. cinerea var. *floridana* (Syntype: BH)	F	F	+	+	w-r			1	+	−	+	s-m	−	+	+	+
V. sola (type: BH)	+	F	+	+	r	B	I	1	+	−	−	s	−	+	+	+
V. rufotomentosa (type: NY)	−	−	+	+	r	B	I	−	+	+	+	s-m	+	+	+	+
V. aranosa (type: PH)	−	−	+	+	r	B	I	−	+	+	±	s-m	−	+	+	+
V. aestivalis var. *aestivalis* 'Pixiola'	−	−	+	+	T-r			1-2	+	+	±	s-m	−	+	+	F
V. aestivalis ssp. *sola* (Rogers 654)	−	−	F	+	w-r	B	I	1-2	+	+	±	s-m	−	+	+	+

Key: F = faintly; + = positive; − = negative; W = white; T = tan; r = refescent; S = 0 − 2 mm long; M = 2 − 5 mm long; B = branched; I = intermittent

The description and specimens cited by Bailey (1934) of taxon number two indicate that Bailey's interpretation of *Vitis sola* apparently included individuals of *V. cinerea* and *V. aestivalis*. The vegetative description applied to both taxa, but the large fruit (usually 9 – 10 mm) is more characteristic of *V. aestivalis*. Examination of the holotype (*Curtiss 4791*, BH!) of *V. sola* by Comeaux revealed that it is within the morphological variation of taxon number one as first suggested by Munson (1887). The paratypes (*Curtiss 4747*, MO! and *Curtiss 6415*, GH!) are *V. aestivalis* var. *aestivalis* and *V. cinerea* var. *floridana*, respectively.

Leaves vary from bearing three to rarely five lobes to unlobed, from nearly entire to heavily toothed margins, from pubescent to puberulent. Color of the vestiture ranges from white, gray, pinkish, tan to rufescent although primarily exhibiting rusty to tan hues.

The epithet *simpsonii* is the oldest name available. However, according to the International Code of Botanical Nomenclature (Stafleu 1983), priority exists only at the same rank. The name *floridana* is the oldest available name at the rank of variety. The recognized nomenclature and synonymy for this taxon are as follows:

1. VITIS CINEREA var. FLORIDANA Munson, U.S.D.A. Div. Pomol. Bull. 3:14. 1890.

Vitis caribaea Munson & authors, non DC.
Vitis simpsonii Munson, Proc. Soc. Pomol. Agric. Sci.8:59. 1887.
Vitis austrina Small, Fl. SE US 755, 1334. 1903.; *nom. superfl.*
Vitis sola Bailey, Gentes Herb. 3:203. 1934. (in part).
Vitis aestivalis ssp. *divergens* Rogers, Proc. Florida State Hort. Soc. 92:280. 1979; *nom. inval.*
Vitis aestivalis ssp. *sola* (Bailey) Rogers, l.c. (in part).
Vitis aestivalis ssp. *simpsonii* Rogers, l.c. (in part)

Taxon number three.

Munson (1909) described this taxon as always bearing leaves with 5-9 rounded lobes, longer internodes, and a later flowering date than other members of series *Aestivales*. This taxon should be considered part of a variable *V. aestivalis* complex. More field research is needed to determine the relationships between several recognized varieties of this species which have non-overlapping distributions, freely intergrade, occupy mostly xeric, sandy soils, and flower before members of series *Cinerascentes*. Other recognized varieties include var. *aestivalis*, var. *lincecumii* (Buckley) Munson, var. *glabra* Bailey, and var. *argentifolia* (Munson) Fernald.

The epithet *simpsonii* is unavailable because it is a later homonym. The epithet *smalliana* is the only legitimate name available. The recognized nomenclature and synonymy for taxon three are as follows:

2. VITIS AESTIVALIS var. **smalliana** (Bailey) Comeaux, comb. nov. *Vitis smalliana* Bailey, Gentes Herb. 3:207. 1934; *Vitis aestivalis* ssp. *smalliana* (Bailey) Rogers, Proc. Florida State Hort. Soc. 92:280. 1979.

Vitis simpsonii Munson, U.S.D.A. Div. Pomol. Bull. 3:12. 1890 (not 1887); *nom. illeg.*

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ERIGERON TURNERORUM (ASTERACEAE), A NEW SPECIES FROM MÉXICO, AND ITS RELATIVES

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ABSTRACT

Erigeron **turnerorum**, a new species from northern Nuevo León, México, is described and illustrated. It is most similar to *E. tenellus*, *E. geiseri*, and *E. tenuis* from the eastern United States and northeastern México and to *E. lobatus* and *E. velutipes* from Arizona and northwestern México.

General collections from México by students, staff, and faculty of the University of Texas continue to yield a number of novelties. The new daisy described below is named for Billie and Gayle Turner, who were members of the expedition that first collected it.

ERIGERON **turnerorum** Nesom, sp. nov. (Fig. 1)

Differt a *E. tenello* DC. caulis foliis et phyllariis glandulosis, pubescentia longissima patula caules, radiis paucis, pappo duplici setae interiores longiores.

Annual herbs from slender taproots. Stems erect, 5 – 25 cm tall, 1 – 2 (– 3) branched, often purplish or reddish at the base, moderately to densely pilose on the lower 2/3 with trichomes 0.6 – 2 mm long, the upper 1/3 strigose with tightly appressed trichomes 0.1 – 0.5 mm long and sparsely and minutely granular – glandular. Leaves moderately pubescent with erect-ascending trichomes and sparsely, minutely granular- – glandular on both surfaces, margins with prominent cilia up to 2.5 mm long; basal leaves 22 – 50 mm long, blades 5 – 14 mm wide, obovate, 2 – 4 lobed with 1 – 3 pairs of serrations on shallow lobes, attenuate to a petiole ca half as long as the leaf, apex rounded to obtuse, apiculate; lower cauline leaves similar to the basal, becoming smaller, entire, and oblanceolate upwards, obscurely subclasping to non – clasping. Heads 1 – 3 (– 8), terminal on peduncles 15 – 60 mm long; involucre hemispheric, 4 – 8 mm wide (pressed); phyllaries in (2 –) 3 – 4 equal to subequal series, outer lanceolate, inner more oblanceolate, all slightly fused basally; outer phyllaries 2.5 – 3 mm long, 0.4 – 0.6 mm wide, stramineous with a greenish midregion and golden mid – vein, surface and margins sparsely but conspicuously minutely granular – glandular, without other trichomes, margins narrowly scarious, receptacles not observed. Ray

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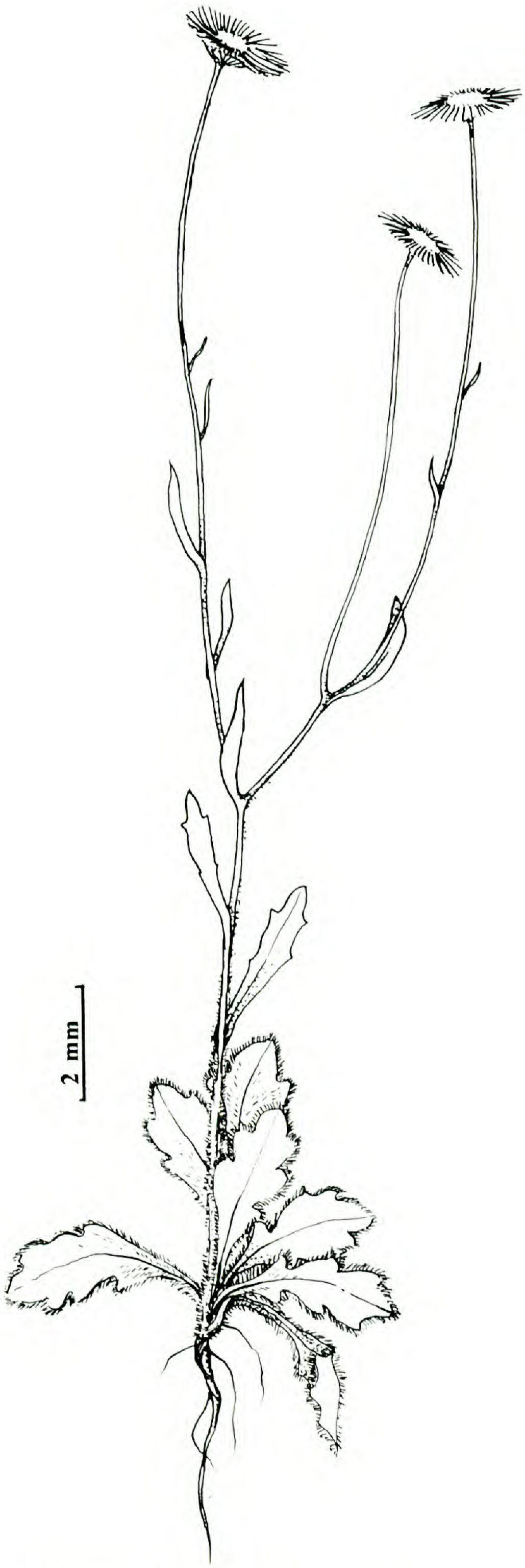

FIG. 1. Habit of *Erigeron turnerorum*.

flowers 20 – 54 in 1 series, corollas white above, lightly bluish – tinged beneath, usually drying with a violet – blue abaxial midstripe, 4 – 7 mm long, ligules 0.6 – 1 mm wide, 3 – 4 – veined, not coiling or reflexing, tube 0.5 mm long, sparsely but conspicuously pubescent with biseriate trichomes; style branches 0.3 – 0.4 mm long. Disc corollas cylindric, 1.5 – 2 mm long, narrowly constricted in the lower 1/5 – 1/4 and noticeably inflated and indurated just above, glabrous to very sparsely pubescent with short, biseriate trichomes; style branches 0.2 – 0.3 mm long, including the blunt – truncate collecting appendages 0.05 – 0.1 mm long. Achenes oblong – obovate, radially compressed, 0.8 – 0.9 mm long, 0.3 – 0.4 mm wide, tan, 2 – ribbed, sparsely strigose; carpopodium a minute, white ring 2 – 4 cells high; pappus of 8 – 13 bristles 0.5 – 1 mm long, shorter than the disc corolla, with numerous but inconspicuous outer setae or very narrow squamellae less than 0.1 mm high. Chromosome number $n = 9$ (Turner 1978).

Known only from the type locality.

TYPE: MÉXICO. NUEVO LEÓN, Mamulique Pass, S of Sabinas Hidalgo on road from Nuevo Laredo to Monterrey; limestone hillside dominated by *Acacia, Yucca, Cordia, Bauhinia*, and *Leucophyllum*, 16 Mar 1976, *M. D. Whalen 338*—population voucher for chromosome count of $n = 9$ (Turner 1978, reported as *E. tenellus* DC.) (HOLOTYPE: LL!).

Additional collections examined: MÉXICO. NUEVO LEÓN: mountains S of Sabinas Hidalgo, 81.6 km S of N.L.-Tam. state line, 59.2 km (37 mi) N of Monterrey on Hwy 85; frequent, going down to dry arroyo at base of hill W of road, by large pull-off area, 13 Mar 1976, *Lewis 228* (LL, TEX); Mamulique Pass on Hwy 85, 37 km S of bridge in Sabinas Hidalgo, on the old road ca 300 m W of Hwy 85, base of steep NW-facing roadcut into limestone; area of *Acacia, Cordia, Prosopis, Yucca, Opuntia, Mahonia, Leucophyllum*, and *Bauhinia, Erigeron calcicola* and *E. modestus* in the same area; 570 m, 23 Mar 1986, *Nesom 5351* (MEXU, TEX).

Erigeron turnerorum is most closely related to a group of species that includes *E. tenellus* DC. and *E. geiseri* Shinners, which occur in Texas and northeastern México, and *E. tenuis* Torrey & Gray of the southeastern United States from eastern Texas northward to eastern Oklahoma and Arkansas and eastward to Mississippi. The new species has been collected only from the southwestern periphery of the composite range of the latter three species (Fig. 2). These taxa share a number of characteristics: (1) prominently nodding buds; (2) relatively small heads; (3) ray flowers that flex upwards at night, "closing" the head; (4) narrow ligules, often with a prominent blue or lilac abaxial midstripe; (5) small achenes, ca 1 mm long; (6) a characteristic pattern of lobing or toothing of the basal leaves; (7) clasping to subclasping cauline leaves; (8) pubescence ascending-appressed on the upper half of the stem, spreading to deflexed below; and (9) stems with a strong tendency to become reddish near the base. The first five of

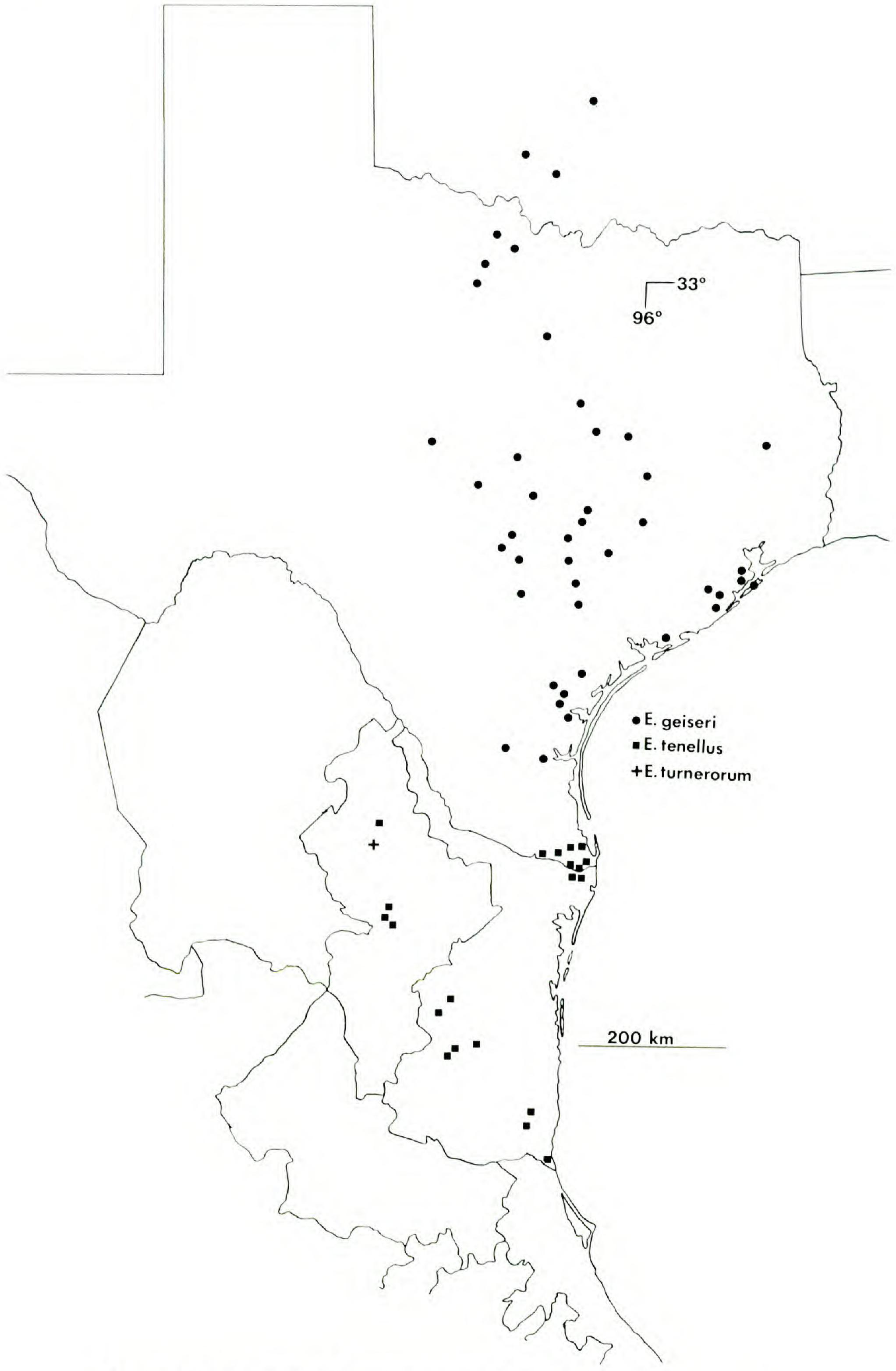

FIG. 2. Distribution of *Erigeron geiseri*, *E. tenellus*, and *E. turnerorum*.

these traits are in common with a broader group of species known as sect. *Oligotrichium*. The midstripes of the rays are sometimes not well-developed in the *E. tenuis* group, where the coloration also may be nearly absent, restricted to the ligule tips, or the whole ligule may appear to be lightly colored abaxially.

Some flowering individuals of *Erigeron turnerorum* are among the smallest I have collected in the genus. The initial collections in 1976 apparently were made during a moist spring because the plants included large individuals and were described as frequent; my recollection in the same season a decade later, but in a dry season, revealed only a few small individuals in the moistest of habitats.

Along with the related small annuals *E. tenellus* and *E. geiseri*, *E. turnerorum* differs from *E. tenuis* in having a slender taproot rather than fibrous roots. The new species is compared to *E. tenellus* in the diagnosis primarily because of the proximity of their geographic ranges. *Erigeron turnerorum* is distinctive in geography and habitat and can be identified by morphological differences in the key that follows.

Erigeron tenellus and *E. geiseri* are included centrally in this discussion not only because of their apparent close relationship to the new species, but also because neither was covered in Cronquist's revision of the genus in North America (1947). Further, these species have well-defined, non-overlapping geographical ranges, but the morphological differences that separate them are relatively small. Since the first citation of *E. geiseri* as a member of the Oklahoma flora (in Comanche Co., Nesom 1979), I have found records of its occurrence in Stephens Co. and Cleveland Co., Oklahoma.

1. Plants with fibrous roots . . . . . *E. tenuis*
1. Plants with slender taproots.
   2. Lower half of stems sparsely pubescent with spreading hairs 0.6 – 2 mm long; at least the upper stems and leaves with minute but conspicuous (under dissecting scope) glands; phyllaries minutely glandular, without other pubescence; rays 20 – 54, ligules 0.6 – 1 mm wide; pappus bristles 0.5 – 1 mm long . . . . . *E. turnerorum*
   2. Lower half of stems sparsely pubescent with spreading to deflexed hairs 0.2 – 0.5 mm long; stems and leaves without glands; phyllaries sparsely pubescent but eglandular; rays 53 – 250, ligules 0.2 – 0.6 mm wide; pappus bristles 1 – 1.8 mm long.
      3. Leaves usually prominently lobed or toothed; rays 95 – 250; pappus bristles 1.4 – 1.8 mm long; outer pappus absent . . . . . *E. tenellus*
      3. Leaves rarely with 1 – 3 pairs of small teeth; rays 53 – 110; pappus bristles 1 – 1.3 mm long; outer pappus present, of scales or setae . . . . *E. geiseri*

Whether through close common ancestry or convergent evolution, two other more widely geographically separated species are similar to *Erigeron*

turnerorum—*E. lobatus* A. Nelson of Arizona and northwestern México and *E. velutipes* Hook. & Arn. (including *E. alamosanum* Rose) of western México. Both are taprooted annuals of sect. *Oligotrichium* and both have similarly lobed basal and lower cauline leaves, a tendency to produce reddish lower stems, and both are typically highly glandular at least on the upper stems, leaves, and phyllaries. In contrast to *E. turnerorum* and its eastern relatives, however, the cauline leaves are not clasping, and both have spreading pubescence on the phyllaries and upper and lower stems.

ACKNOWLEDGMENTS

Records for the distribution map are primarily from TEX-LL with additions from GH, OKLA, OS, RM, SMU, and UTEP. I thank Jim Henrickson for constructive comments on the manuscript and Marcella Nesom for the illustration.

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LECTOTYPIFICATION OF *CYANOCOCCUS CUTHBERTII* SMALL (ERICACEAE)

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ABSTRACT

Cyanococcus cuthbertii Small is lectotypified from discordant elements.

In studying the genus *Vaccinium* L. (Ericaceae) in South Carolina, it was discovered that the type sheet of *Cyanococcus cuthbertii* Small bears two discordant elements. To comply with Art. 9.2 of the ICBN, lectotypification of this name is required.

CYANOCOCCUS CUTHBERTII Small, Man. Southeast. Fl. 1015, 1507. 1933.

Vaccinium virgatum Ait., Hort. Kew ed. 1. 2:12. 1789.
Vaccinium amoenum Ait., Hort. Kew ed. 1. 2:12. 1789.
Vaccinium ashei Reade, Torreya 31:71. 1931.
Vaccinium cuthbertii (Small) Uphof, Mitt. Deutsch. Dendrol. Ges. 48:19. 1936.

The discordant elements on the type sheet are (A) a twig in anthesis, just leafing out, mounted on the right half of the sheet: GEORGIA, Augusta: swamp along Rice's Creek, 29 Mar 1900, *A. Cuthbert 259*, and (B), a leafy twig bearing black berries, same locality, 6 Jun 1900, same collector, same number, mounted on the left half of the sheet (LECTOTYPE: here designated, NY!). The collector noted on his label that he was unsure that the two specimens came from the same plant. Obviously, they did not, as will be demonstrated below.

Element A was annotated by W. H. Camp in 1942 to be a segregate of *Vaccinium elliottii X tenellum*. I agree. Camp (1945) states that the name *Cyanococcus cuthbertii* has been applied to such segregates, which are frequent.

Element B was determined by Camp (1945) to represent a specimen of *Vaccinium caesariense X tenellum*. I do not agree. The leaves bear stout stalked glands (called "spine-like hairs" in the description of *Cyanococcus cuthbertii*) on the undersurface veins, in the manner of *V. ashei* Reade (which I consider to be a phase of *V. virgatum* Ait.). The leaves are strongly reticulate-veiny on the undersurface, again after the character of the *V. ashei* phase of *V. virgatum*. The leaves have irregularly serrulate thickened glanduliferous

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margins, and though small (up to 3.5 cm long), are within the limits of *V. virgatum sensu* Rehder (1940), which includes *V. amoenum* Ait. The leaves are glabrous except for the numerous stiff glands. The squarrish twigs are also glabrous. The leaf bud scales are black, each with a distinct uncinate arista about 1 mm long. The berry is black. *Vaccinium virgatum* (*V. amoenum*, *V.. ashei*) is most often more or less pubescent, but glabrescent and glabrous phases occur. These are known from the Savannah River basin from whence the lectotype was collected. I determine that the lectotype, element B on the type sheet, is *Vaccinium virgatum*.

The description of *Cyanococcus cuthbertii* is only slightly garbled with characters of the two elements to which this name has been applied. By far, Small's description applies more to element B than to element A. It for this reason element B was selected as the lectotype. It is fortuitous that it was not obligatory to select element A as the lectotype because this would have required that *Vaccinium cuthbertii* (Small) Uphof be proposed *pro sp.* for the frequent segregates of *V. elliottii X tenellum*. This would have resulted in a clumsy nomenclatural situation.

ACKNOWLEDGMENT

I gratefully appreciate the kindness of the New York Botanical Garden for lending me the type sheet.

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A MORPHOMETRIC COMPARISON OF *HYMENOCALLIS PALMERI* AND *HYMENOCALLIS FLORIDANA* (AMARYLLIDACEAE) IN SOUTHERN FLORIDA

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ABSTRACT

Hymenocallis palmeri S. Watson and *H. floridana* (Raf.) Morton, closely related species which grow sympatrically in the wetlands of Florida, were studied morphometrically to determine whether they could be consistently distinguished. Information was collected on leaf width and seven characters of the inflorescence from several populations in southern Florida. Analysis of this data suggested that the two species were separable on the basis of flower size and leaf width. Differences in habitat and blooming period were found to corroborate the separation of the two species.

INTRODUCTION

Twenty-two species of *Hymenocallis* have been described from or attributed to Florida during this century (Small 1933; Traub 1962; Flory 1978). They have primarily been distinguished from one another on the basis of floral characteristics which are poorly, or not at all, preserved on dried specimens. Consequently, the application of available names and even the number of species involved has been confused in recent years (as shown by the divergent treatments in Sealy 1954; Traub 1962; Long & Lakela 1971; and Wunderlin 1982). Godfrey and Wooten (1979) refused to treat the genus due to this confusion.

One species which has been consistently recognized is *H. palmeri* S. Watson. This species has been characterized by having a single flower on each inflorescence. Plants with two or more flowers per inflorescence have been assigned to other species. Sealy (1954) suggested that *H. palmeri* might represent a depauperate form of *H. rotata* (including *H. floridana*) but let it stand as a separate species. The existence of two-flowered specimens within populations of typical (one-flowered) *H. palmeri* led me to study more closely the relationship between the one-flowered and two-flowered plants in southern Florida.

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MATERIALS AND METHODS

The *Hymenocallis* species under study are bulbous herbs inhabiting seasonally inundated prairies (glades). They are found in glades with average periods of yearly inundation from one month to over six months. Those prairies with shorter periods of inundation are typically dominated by *Muhlenbergia filipes* M.A. Curtis and stunted plants of *Cladium jamaicense* Crantz. The more deeply flooded prairies are dominated by nearly monospecific stands of dense *Cladium*. Flowering plants of both species are most commonly found in burned sites. As the dominant vegetation reestablishes a continuous cover following fire, flowering of the *Hymenocallis* becomes less common. Few leaves are present on a plant at any one time, and I have never observed more than a single inflorescence on a bulb. Flowers open in the evening and remain open through the following day. Rarely, flowers remain open a second day.

Flowers of *Hymenocallis palmeri* (Fig. 1) are born erectly or sub-erectly on a peduncle (scape) which normally exceeds the leaves in length. Two bracts subtend the inflorescence and a single additional bract is found below each flower. The ovary may be sessile or pedicellate, with the former condition much more common. The perianth is six-parted with three sepals and three very similar, but distinguishable, petals. The lower portions of the sepals and petals are connate and form a long, slender tube. Above the tube, the free perianth lobes spread out radially. These perianth lobes are light green in color with the petal lobes lighter than the sepal lobes. The lower portions of the staminal filaments are connected by a thin membrane of tissue, forming a staminal cup. This cup, which is characteristic of the genus, is variably shaped. The filaments extend beyond the cup in the species under consideration. The anthers are held more-or-less rigidly at a level below that of the exserted stigma. Flowers of *H. floridana* have the same structure but the color of the perianth lobes is white.

Fresh flowers from several sites in southern Florida (Table 1, Fig. 2) were examined, usually the morning after they opened. Measurements (Table 2, Fig. 1) were made in the field, or flowers were removed from the plants and measured in the lab within two hours. A few measurements were also taken from cultivated plants which bloomed during the course of this investigation. Most measurements were made during the summer of 1984. No change was noted in size as the flowers aged, but some floral parts began to lose shape after the first morning and characters like anther length and perianth lobe width quickly became impossible to measure accurately. Other data collected, but not utilized in this study, included the number of ovules in each locule of the ovary, length of the lower inflorescence bract, pedicel length (when present), and the shape of the peduncle. Bract length

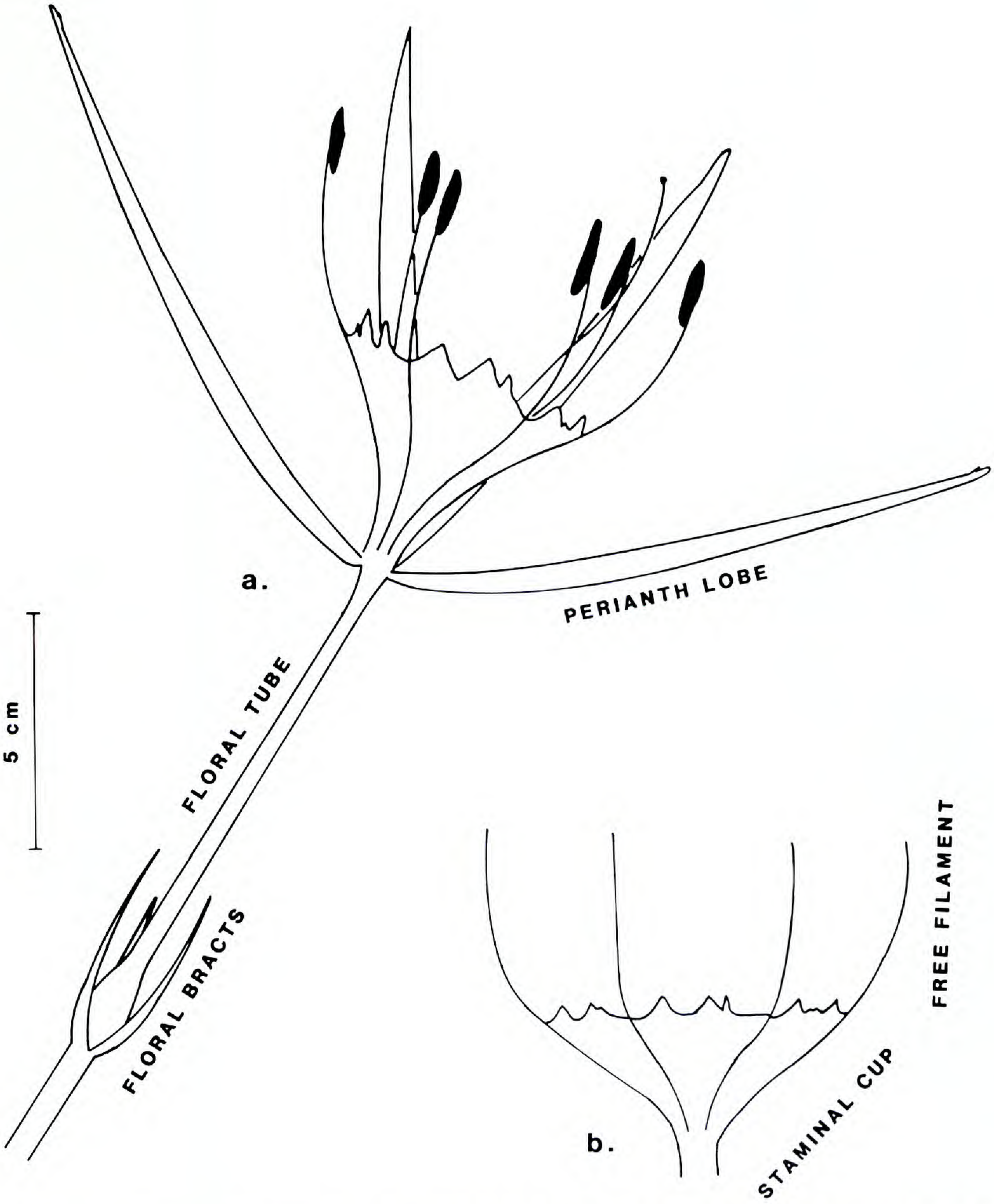

FIG. 1. a) Flower of *Hymenocallis palmeri* (Glade 5, Long Pine Key, Everglades National Park, July 1985) with two tepals facing the viewer removed. Floral characters were measured as shown. Sepal and petal lobe widths were measured at the widest points, at the position shown in the figure. The lowest (longest) floral bract was measured. b) Staminal cup of a flower from the same population collected on the same day, showing the variablility in this structure.

TABLE 1. Location of *Hymenocallis* populations sampled during the current study. The number of individual plants for which morphometric measurements were taken is given. The number of individuals included in the PCA analysis is given in parentheses when different from the number measured.

SPECIES	LOCATION	NUMBER OF INDIVIDUALS MEASURED
H. palmeri	Glade 1.5 km W of Taylor Slough, Everglades National Park	47
	SW 288 St - 237 Ave, W of Homestead	31
	SW 88 St - 137 Ave, Kendall	17
	Glade 6, Long Pine Key, Everglades National Park	5
H. floridana	Gaging Station P36, near Sisal Pond, Everglades National Park	25
	Glade 5 (farmed area), Hole-in-the-Donut, Everglades National Park	9
	Taylor Slough Bridge, Everglades National Park	6 (0)
	SR 27, 4 mi S of intersection with US 27	5 (2)
	Gaging Station P33, Shark Slough, Everglades National Park	2

and pedicel length measurements could only be made on a few inflorescences and were excluded from the analysis to preserve sample size. Ovule number and peduncle shape were recorded for comparison with species in other alliances of *Hymenocallis* (Traub 1962); they did not differ between *H. palmeri* and *H. floridana*. If two flowers in an inflorescence were open, they were measured separately and recorded with information on their relative age.

Although several characters of the staminal cup (edges spreading or erect, number and placement of teeth along the margins of the cup) have been used to define species in the past, they were not considered in the current study. Cup shape was disregarded because it was found to be too variable within populations. Tooth patterns along the margins of the cup seem to be constant within populations, but they did not vary significantly between the groups under study. In any case, the characters of the staminal cup are rarely seen in pressed specimens.

Measurements from 100 individuals of *H. palmeri* representing four populations and 38 individuals of *H. floridana* representing four popula-

tions were used for the initial morphometric analysis. Seven floral characters (floral tube length, sepal lobe length and width, petal lobe length and width, staminal cup length, and free filament length) were entered into the principal components analysis (PCA) routine of SPSS/PC. This is a version of the Statistical Package for the Social Sciences (SPSS) configured to run on an IBM PC/XT.

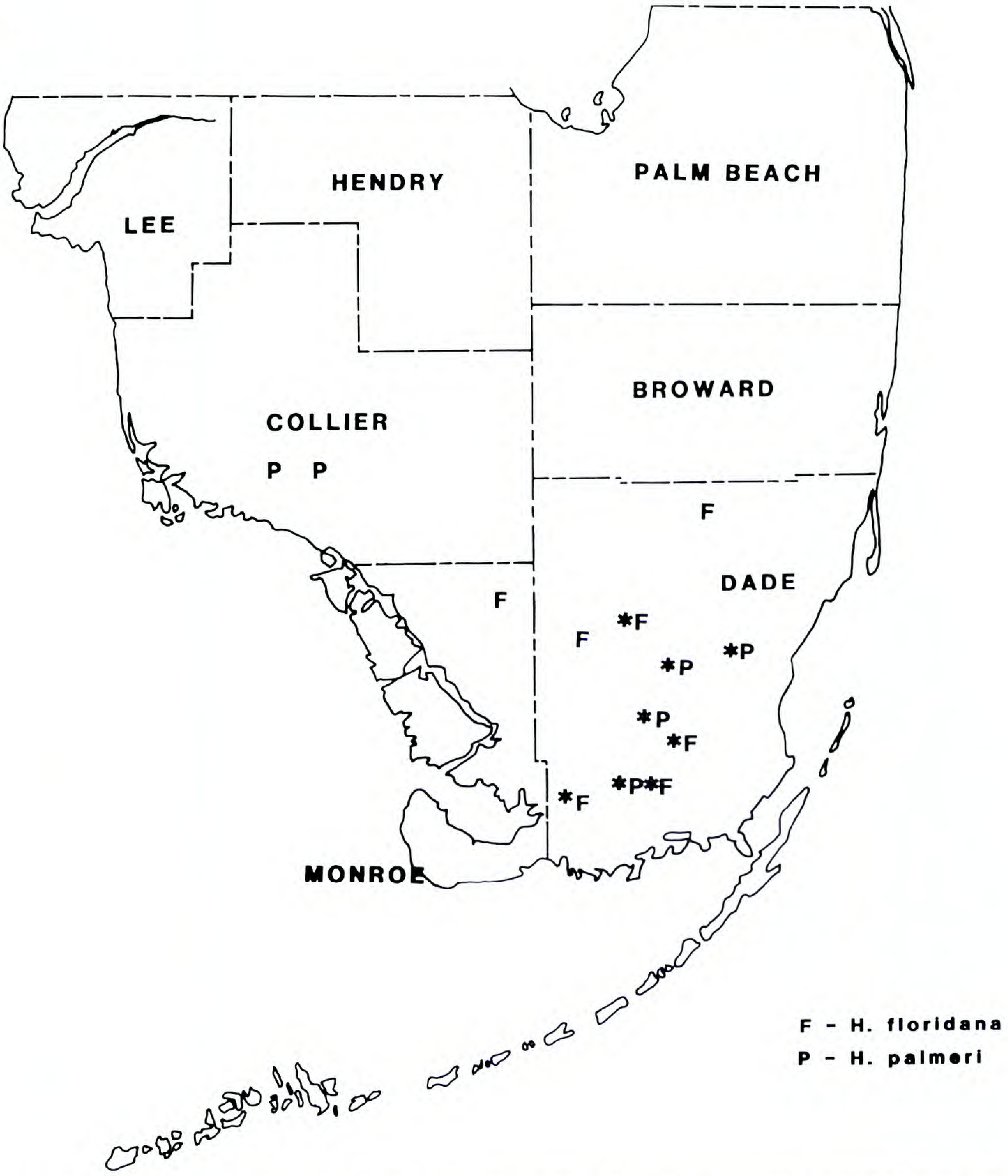

FIG. 2. Populations of *Hymenocallis floridana* (F) and *H. palmeri* (P) examined or noted during this study. Morphological measurements were made in populations noted by an asterisk (see Table 1 for exact locations).

TABLE 2. Characters used in the morphometric comparison of *Hymenocallis floridana* and *H. palmeri*. Group means and their standard deviations are given. The measurements made for Floral tube length, Staminal cup length, and Free filament length are illustrated in Figure 1.

CHARACTER	H. FLORIDANA	H. PALMERI
Leaf width (mm)	14.80 ± 2.70	8.59 ± 1.69
Floral tube length (cm)	6.90 ± 1.32	11.60 ± 1.90
Sepal lobe length (cm)	9.92 ± 1.01	12.20 ± 1.50
Sepal lobe width (cm)	0.62 ± 0.06	0.67 ± 0.12
Petal lobe length (cm)	9.59 ± 0.98	11.90 ± 1.50
Petal lobe width (cm)	0.82 ± 0.11	0.78 ± 0.12
Staminal cup length (cm)	3.12 ± 0.52	3.86 ± 0.52
Free filament length (cm)	3.25 ± 0.46	3.73 ± 0.49
Anther length (cm)	1.94 ± 0.11	2.10 ± 0.29

For initial analysis, populations of *Hymenocallis* were divided into two groups on the basis of flower number per inflorescence. If the normal number of flowers per inflorescence in a population was one, all plants in that population, including those with two flowers, were assigned to the species *H. palmeri*. If most of the plants in the population had two flowers per inflorescence, all plants in the population were assigned to *H. floridana*. In all populations examined, the plants were almost entirely either one or two flowered. Plants with the "wrong" number of flowers never made up more than 10% of the population.

H. floridana is used as the name for the two-flowered plants because it has been used in that sense in recent years (Traub 1962). Given the uncertainty surrounding this and all other early names in the genus, however, it is best to keep in mind that the name is being used as a convenient label and is not well-founded.

RESULTS AND DISCUSSION

PCA scores were calculated for each flower examined. Using identifications obtained by the procedure outlined above, a plot of each flower against the individual PCA axes was constructed. These plots showed a good separation of the putative species along PCA axis one (Fig. 3). There was overlap, indicating that the groups were not consistently distinguished from each other on the basis of the morphological characters used. No separation was seen along the other two PCA axes examined. Flowers were smaller on the average in the plants assigned to *H. floridana*, but a continuous gradation was found between the two groups for every combination of floral characters (Fig. 4).

Examination of group means (Table 2) and correlations between characters suggested that floral tube length and leaf width provided the

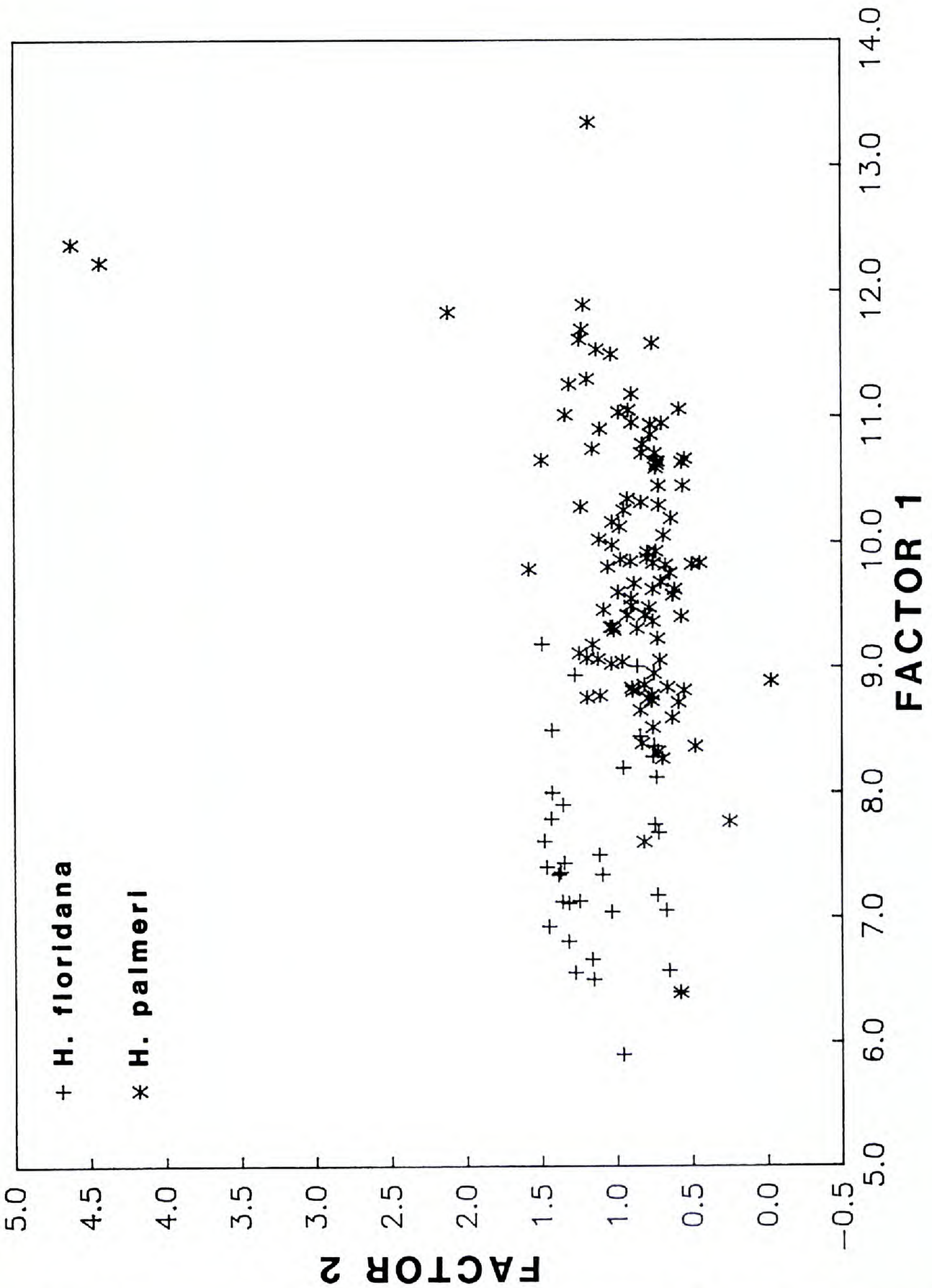

FIG. 3. Projections of individual flowers onto the plane of the first two PCA axes. Forty-nine percent of the variance in the sample was explained by the first principal component (Factor 1). An additional eighteen percent of the variance was explained by the second principal component (Factor 2).

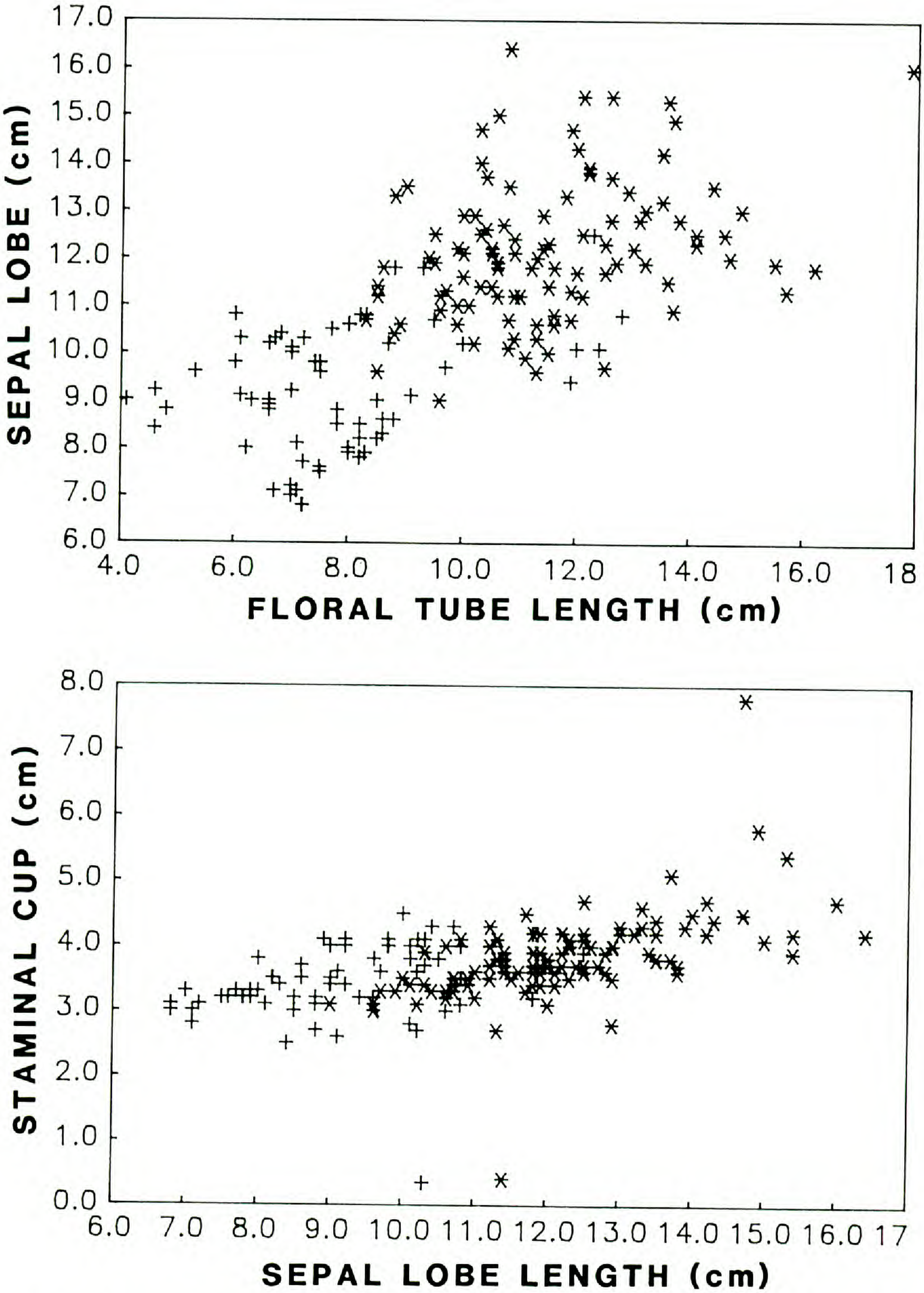

FIG. 4. Two scatter diagrams of floral characters plotted against each other. a) Sepal lobe length vs. Staminal cup length and b) Floral tube length vs. Sepal lobe length. These diagrams show the continuity in flower proportions.

TABLE 3. Comparison of characters supporting the distinctness of *Hymenocallis palmeri* and *H. floridana*. Individual specimens may deviate from the limits listed for leaf widths or floral tube lengths. In those cases, consideration of the remaining characters should allow unambiguous identification of the species.

CHARACTER	H. FLORIDANA	H. PALMERI
Blooming season	April – June	July – September
Sepal color	White	Green
Habitat	Wet prairie	Dry prairie
Rhizomes present	Yes	No
Floral tube length	< 9.5 cm	> 9.5 cm
Leaf width	> 12 mm	< 12 mm

best means of distinguishing the two groups. When these values were plotted, they separated the two groups (Fig. 5). Overlap was extensive between populations within each of the two groups except in the case of the two points representing *H. floridana* which lie nearest the cloud of *H. palmeri* points. These two points came from a single plant in an otherwise unsampled population. No evidence for clinal variation from population to population was seen. Altogether, the pattern of scatter supported the hypothesis that two discrete species were present. Further evidence for the distinctness of the two groups was found by considering their distribution and blooming periods (Table 3). An analysis of cases in which plants had the 'wrong' number of flowers showed that they were morphologically typical of the population with which they grew, and unquestionably belonged to the same species. Two-flowered *H. palmeri*, with all the attributes listed in Table 3, were found, as were one-flowered *H. floridana*.

A difference in blooming periods became evident during the course of the present study. In the few populations I could follow closely, *H. floridana* had finished blooming before *H. palmeri* started. An examination of herbarium specimens at Fairchild Tropical Gardens and the field notes of G. N. Avery corroborated this observation. Opportunities for gene exchange between the two groups, thus, seem to be limited by non-overlapping blooming periods. The habitat difference noted would also limit the opportunity for gene exchange, but I did find sites where the two species were growing within 100 meters of each other (in the vicinity of Taylor Slough Bridge, Everglades National Park, *H. palmeri* was common in the glades peripheral to the main drainage channels while *H. floridana* was found in wet pools along the channels).

Two other characters also corroborated the separation of the two taxa. Color of the perianth lobes was always light green on plants placed in *H. palmeri* while the lobe color was white, or nearly so, on plants of *H. flori-*

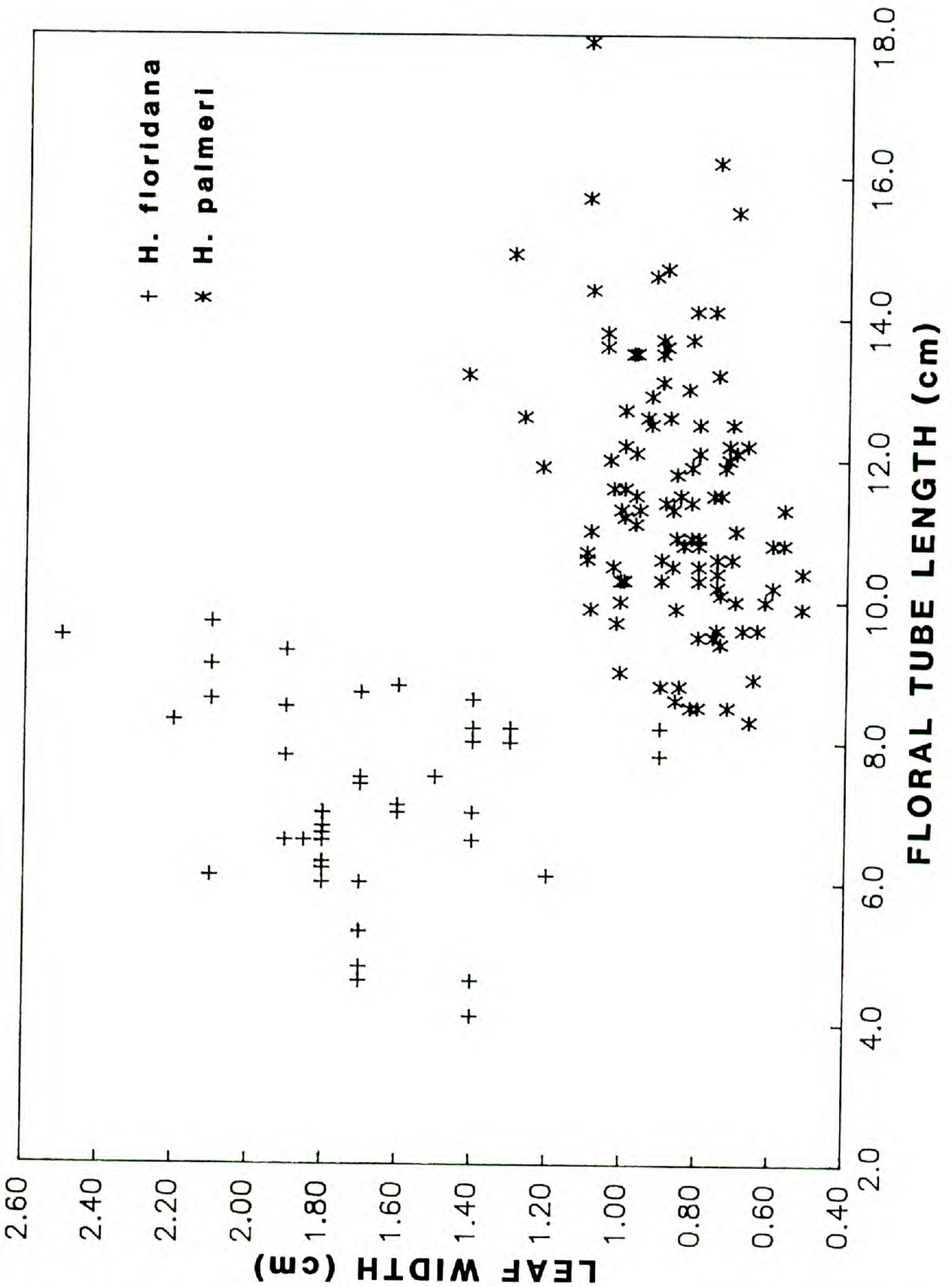

FIG. 5. Scatter diagram of floral tube length against leaf width, showing the separation of *Hymenocallis floridana* and *H. palmeri* by these characters.

dana. Rhizomes were found on large plants in every population of *H. floridana* but were never observed in populations of *H. palmeri*. Both of these characters have been noted previously (Small 1933; Sealy 1954) and used to separate these or closely related species.

While it now seems evident that there are two species of *Hymenocallis* in the glades of southern Florida, it is not so clear how these southern populations relate to those found farther north in the state. Cursory examination of specimens at the University of Florida Herbarium (FLAS) and discussion with Gerald L. Smith suggests that the typically one-flowered species (including *H. palmeri*) show decreasing flower size as one travels north in the state, while the typically two-to-few flowered species (including *H. floridana*) show increasing flower size. Detailed examination of *Hymenocallis* populations from throughout Florida will probably be necessary to reach an understanding of this pattern.

The use of flower number per inflorescence for recognizing species should be de-emphasized since individual plants with the "wrong" number occur often enough to create much confusion.

ACKNOWLEDGMENTS

Dr. George Dairymple of Florida International University provided guidance in the field of multivariate morphometrics during the initial stages of this study. Alan Meerow of the University of Florida and Gerald L. Smith of Wake Forest University provided useful reviews of the manuscript.

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BOOK REVIEWS

DICTIONARY OF WORD ROOTS AND COMBINING FORMS. 1960. 11th printing, 1971. Borror, Donald J. Mayfield Publishing Co. 134 pp. + v. Paper, $5.95.

This paperback is one that is still available after eleven printings and 25 years. In the field of taxonomy and other areas of biology, this dictionary is quite appropriate for faculty and student reference in spite of all the new advances. With the original meanings of the prefixes and suffixes, one is able to determine the meaning of the words without consulting one of the large unabridged dictionaries. The Chapters are 1) How to Use This Dictionary, 2) Dictionary of Word Roots and Combining Forms, 3) Formulation of Scientific Names, 4) Transliteration of Greek Words, and 5) Some Common Combining Forms. On page 114, in reference to the capitalization of the species epithets of plants, it is now recommended that all begin with a small letter.

For students striving to learn the meanings of the roots, it is often quite boring to study lists. One method of studying this type of material would be to suspend the recommended rules in the popular game of "Scrabble" and to substitute this dictionary in the place of the standard type. This biological dictionary is an excellent reference and very inexpensive.—WFM

COFFEE: BOTANY, BIOCHEMISTRY AND PRODUCTION OF BEANS AND BEVERAGE. 1985. Clifford, M. N. and K. C. Willson, eds. 457 pp, illustrated. Croom Helm, Provident House, Burrell Row, Beckenham, Kent BR3 1AT, England. ISBN 0-7099-0787-7. Hbk, £40.00.

This comprehensive text on coffee will be of interest to a wide range of people all over the world concerned with botany, agriculture, food science and technology. The book is full of data that is a delight to scan and read through. The table of contents: 1) A history of coffee, 2) Botanical classification of coffee, 3) Coffee selection and breeding, 4) Climate and soil, 5) Physiology of the coffee crop, 6) Mineral nutrition and fertiliser needs, 7) Cultural methods, 8) Pest control, 9) Control of coffee diseases, 10) Green coffee processing, 11) World coffee trade, 12) The microscopic structure of the coffee bean, 13) Chemical and physical aspects of green coffee and coffee products, 14) The technology of converting green coffee into the beverage, 15) The physiological effects of coffee consumption, Glossary and Index. A must for any major library and serious researcher on any aspect of coffee; a delight to have on your book shelf whether at home, office or library. BLL

A TAXONOMIC REEVALUATION OF *GOSSYPIANTHUS* AND *GUILLEMINEA* (AMARANTHACEAE)

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ABSTRACT

Gossypianthus and *Guilleminea* are recognized as distinct genera. Two species of *Gossypianthus* are recognized, *G. brittonii* restricted to Cuba, and the more widespread *G. lanuginosus* with two varieties: var. *lanuginosus* from Hispaniola, Oklahoma, Texas and northeastern México; and var. *tenuiflorus* from Oklahoma, eastern and coastal Texas. Two species of *Guilleminea* also also recognized, *G. elongata* from Uruguay, and *G. densa* with three varieties: *G. densa* var. *densa* in South America from Ecuador to Argentina and naturalized in Queensland, Australia and southern Africa; var. *aggregata* in Texas, New Mexico, south to Oaxaca, México; and var. *gracilis* from high elevations in northern Argentina and adjacent Bolivia.

INTRODUCTION

In 1967 Mears published a revision of *Guilleminea* Kunth in H.B.K. (Amaranthaceae) in which he included *Gossypianthus* Hook. as a subgenus. My observations made during preparation of a treatment of Amaranthaceae for the Chihuahuan Desert Flora showed the taxa were so fundamentally different in floral structures that a congeneric treatment could not be supported. Further studies on the species within the two genera revealed the necessity of a complete reevaluation of the taxa.

The genus *Guilleminea* was erected by Kunth in Humboldt, Bonpland and Kunth (1823) based on a collection of Humboldt and Bonpland from Quito, Ecuador. The species upon which this name is based, however, was previously published from a duplicate specimen given to Willdenow who was designated to work up the voluminous Humboldt and Bonpland collections. Willdenow's brief notes were published after his untimely death in 1812 by Roemer and Schultes in 1819 (see McVaugh 1955). The combination *Guilleminea densa* (Willd. in Roem. et Schult.) Moq. was made by Mouqin-Tandon (1849) in deCandolle's Prodromus. The genus is here considered to consist of two species; one is widespread in the New World with an amphitropical distribution and occurs from Arizonia, Oklahoma south through Texas to south-central Mexico in North America and from Ecuador to Argentina in South America and is naturalized in southern Africa and northeastern Australia (Fig. 4). The other species is

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known only from the type collection in Uruguay. As noted by Uline and Bray (1895), Necker (1790) had earlier used the name *Guilleminia* (with an *ia* ending) as a later synonym of the genus *Voltomita* Aubl. (Cornaceae). Necker, however, used the name as a mononomial for his "species naturales" and his mononomials are expressly rejected as generic names by Article 20.4(b) of the International Code of Botanical Nomenclature (Voss 1983; See also Stafleu and Cowan 1981, p.704). In anticipation of its rejection Uline and Bray (1895) conservatively recognized *Guilleminea* (with an *ea* ending) Kunth in H.B.K. Small (1903), however, renamed the genus *Brayulinea* Small, and this was accepted by Standley (1917) and by Schinz (1934). The passage of Article 20.4b (example 11) of the International Code of Botanical Nomenclature, however, reinstates the generic name *Guilleminea* Kunth in H.B.K. as noted by Mears (1967).

Gossypianthus was described by W.J. Hooker from Drummond's Texas collections in 1840. The genus is here considered to consist of two species; one ranges from Oklahoma, through Texas and adjacent Mexico, and in Hispaniola; the other is restricted to Cuba (Fig. 4).

Within the Amaranthaceae, the two genera clearly fit into the tribe Gomphreneae Endl. or subfamily Gomphrenoideae (Endl.) Schinz as they have 1-thecal, 2-locular anthers, ovaries with single ovules pendulent from an elongate, arching, basally-derived funiculus, but their treatment within this group has varied.

A representative sampling of past treatments shows that Moquin-Tandon (1849) in his Prodromus treatment placed both genera at the begining of the tribe Gomphreneae Endl. next to *Iresine*. Bentham and Hooker (1880) placed *Guilleminea* at the base of the Gomphreneae next to *Cladothrix* Nutt. (now *Tidestromia* Standl.) and *Gossypianthus* near *Alternanthera* Forsk. Standley (1917) in his North American Flora treatment followed Schniz (1893) in placing *Guilleminea* (as *Brayulinea*) in the tribe Brayulineae next to the Gomphreneae while placing *Gossypianthus* in the tribe *Gomphreneae* near *Tidestromia*, *Pfaffia* Mart. and *Achyranthes* L. Schnitz (1934) recognized *Brayulinea* in his subfamily Gomphrenoideae as tribe Brayulineae, subtribe Brayulineinae next to subtribe Tidestromiinae while *Gossypianthus* was placed in his tribe Gomphreneae subtribe Froelichiineae between *Pfaffia* and *Alternanthera* Forsk.Mears (1967) recognized the two taxa as subgenera of a single genus *Guilleminea*.

Guilleminea and *Gossypianthus* are very similar in vegetative features (Figs. 1A, 2A). Both are procumbent perennials with fibrous, somewhat fleshy roots.They both produce a basal rosette of leaves and their lateral stems often have woolly or villous internodes. Leaves may be crowded or more remote along stems, are opposite, exstipulate, subequal, connate

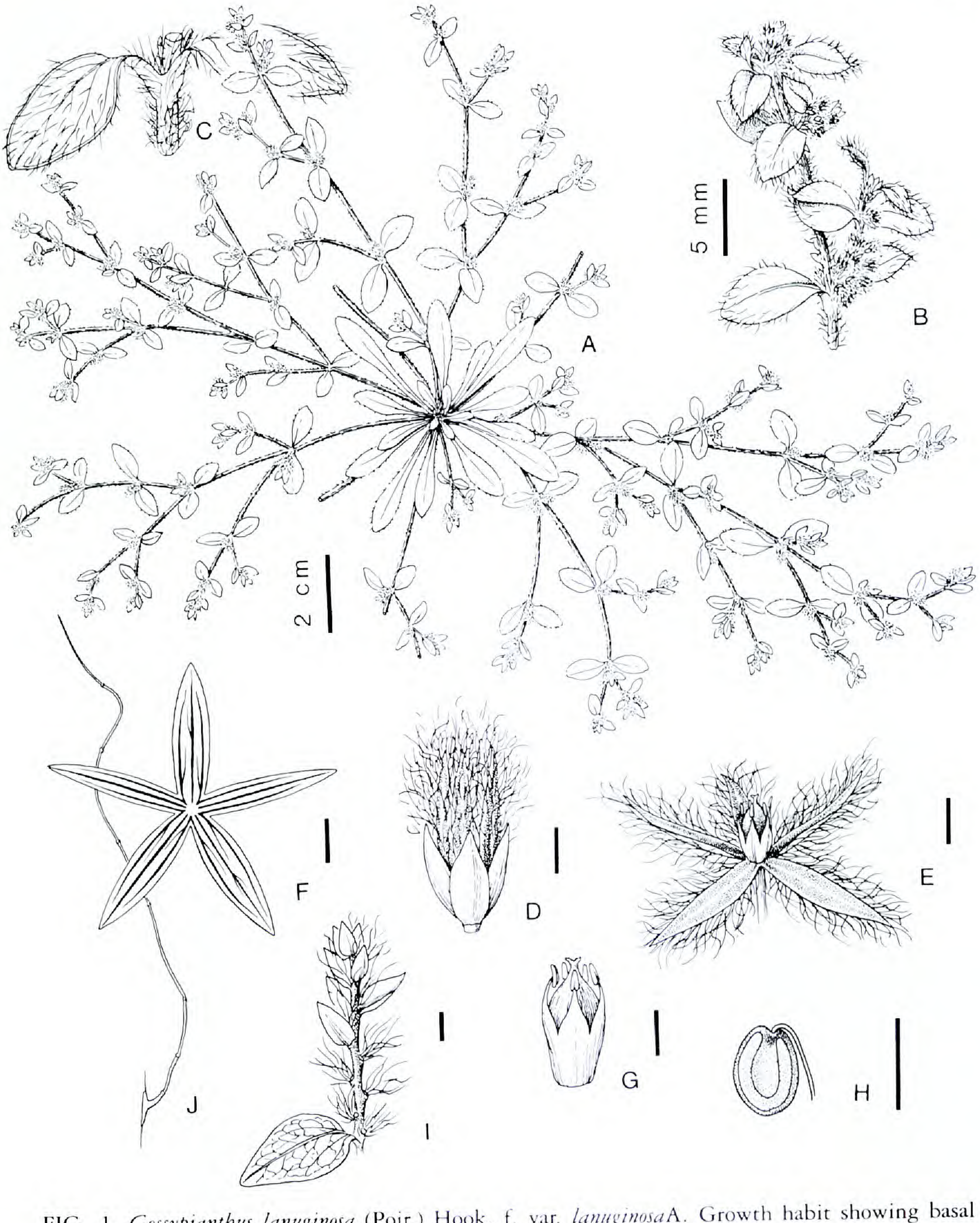

FIG. 1. *Gossypianthus lanuginosa* (Poir.) Hook. f. var. *lanuginosa*A. Growth habit showing basal persistent rosulate leaves, spreading procumbent stems.B. Young stem showing arrangement of leaves, inflorescences. C. Opposite, basally-connate leaves showing long trichomes (A – C from *Pringle* 689 (GH). D. Closed flower showing outer membranous bract, paired bractlets and densely woolly-villous calyx. E. Open flower showing spreading sepals. Sepals actually reflex strongly at very base. Two narrow sepals have basal concavities that fit around the margins of the ovary, while 3 broader sepals are flat. Note separate filament tube. F. Diagramatic representation of venation of sepals. All sepals have 3 traces, these are branched on 3 broader sepals.G. Ovary surrounded by monadelphous stamens. H. Immature seed with attached funuculus. I. Spicate inflorescence axis showing some persistent bracts and axillary tufts of persistent long trichomes. J. Structure of trichomes on outer calyx surface and inflorescence axis ca. 1 mm long. C – I based on studies of several specimens. Magnifications of A – B as indicated, of C equal B, bars in D-I all equal 1 mm. Drawn by Bobbi Angell.

basally around the stems, (Figs. 1B, 2B – C, 3) are mostly oblong-obovate to ovate with broad petioles with Kranz-type internal anatomy, and are frequently glabrate above, more persistently villous beneath. Both genera tend to produce clusters of axillary leaves and flowers in axillary glomerate spikes (Figs. 1B, 2B, 3). In both, paired bracteoles fall with the flowers, the bracts-bracteoles are whitish, membranous, glabrous, and the outer calyx surface is very densely woolly with long, uniseriate, multicellular trichomes 2 – 5 mm long. The arrangement of the flowers in the inflorescences are also very similar (Fig. 3A – B). From a distance they are very difficult to distinguish and they are sometimes confused with procumbent species of *Alternanthera* and *Achyranthes*.

But significant differences in vegetative and floral morphology do occur. Vegetatively the basal rosette leaves of Gossypianthus are persistent and rather prominent (Fig. 1A), while those of *Guilleminea* are much smaller and normally abscise by flowering time.

The greatest differences between the two taxa occur in flowers. In *Gossypianthus*, the perianth consists of five separate, subequal sepals (Fig. 1D – F) each with 3 separate veins from the base. Stamens are separate from the calyx, ovary and filaments are connate into a shallow, cup-like, basal tube 0.2 – 0.5 mm high around the ovary, and the free filaments taper to a tip below the introrse anthers (Fig. 1E,G). The perianth lobes are often green between the three veins and have rather narrow scarious margins. All five sepals are of approximate equal length but the two inner sepals are distinctly narrower and more keeled than the other three sepals (Fig. 1E – F). The ovary is slightly compressed and its margins fit into the concavity on the inner surface of the two narrower, keeled sepals. Before and after flowering time sepals are erect and closed around the ovary. At anthesis the tissue at the inner sepal base swells up, causing the flower to open widely with sepals deflexing above the base. In post-anthesis flowers the inner portion of the sepals becomes relatively indurate. Pollen is produced at about the level of the stigma, the ovary later elongating. Nectary location and nectar production are not known. At maturity, an abscission layer develops at the flower base on the short pedicel; seeds fall with the perianth and paired bracteoles and the fruit is dispersed by the long exterior perianth hairs (Fig. 1D). Perianth structure (i.e. of five separate, 3-veined sepals) is basically similar to other related genera in the tribe i.e. *Pfaffia*, *Alternanthera*, and *Achyranthes*.

Flower structure in *Guilleminea* is fundamentally different from that of *Gossypianthus* and contains features unique to the family. In *Guilleminea* the perianth consists of a basal, slightly ampliate, scarious tube topped by five, essentially equal, oblong, oblong-oblanceolate to lanceolate, acute to

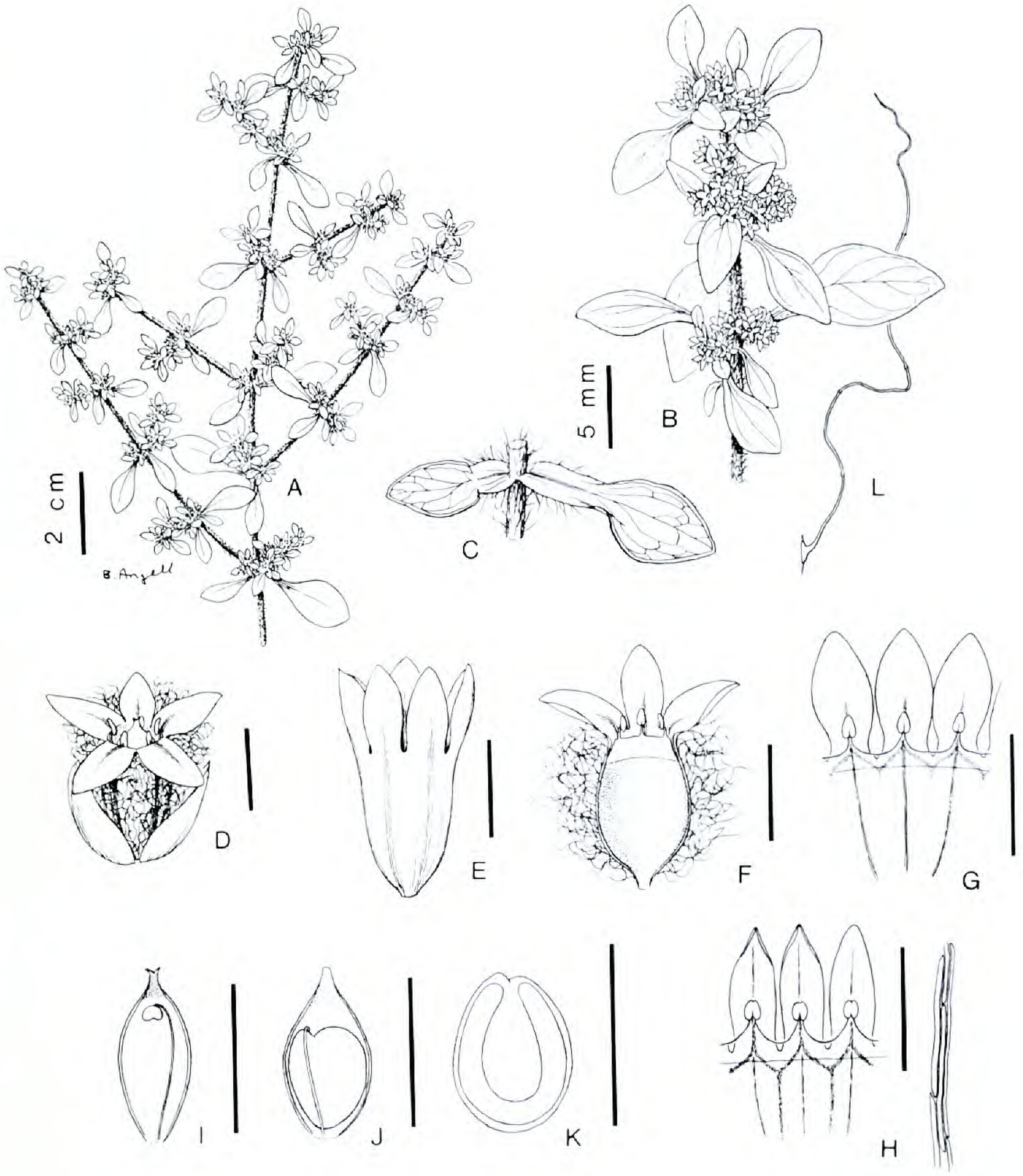

FIG. 2. *Guilleminea densa* (Willd. in Roem. & Schult.) Moq. in DC. A. Growth habit showing only a portion of stem. This plant has much larger leaves than characterisitc for this species. B. Young stem showing arrangement of unequal, opposite leaves and clusters of open flowers. C. Opposite, basally connate unequal leaves with characteristic broad, achlorophyllous, winged petiole-like bases. D. Open flower at anthesis showing paired membranous bractlets, dense trichomes on outside of calyx (shown enlarged in L), reflexed sepals, opposite stamens, exposed ovary. E. Shape of preanthesis calyx with outer trichomes removed. F. Inner view of expanded fruiting calyx showing attachment of monadelphous stamens (at horizontal line), upper free filaments and outer trichomes. G. Inner view of flattened calyx of North American *G. d.* var. *aggregata* showing position filament tube and anthers; distinct perianth fiberous system is showed by stippling along midvein at base of calyx lobes and in a horizontally oriented V-shaped pattern between sepals. Note shortness of lower extension down calyx tube. H. Inner view of flattend calyx of South American *G. d.* var. *densa* showing filament tube and anthers; here perianth fiberous system tends to form distinct downward extensions in calyx tube making tube appear 10 veined. Structure of fibers is indicated on right. I. Young ovary showing ovule on elongated, basally attached funuculus. Note bilobed style. J. Fruiting ovary with seed. K. Seed ca. 0.9 mm long. L. Structure of trichome from outer calyx surface ca. 1.8 mm long. A – C from *G. d.* var. *aggregata; Parry & Palmer 788 1/2* (GH), D – K based on studies of several specimens. Magnifications of A – B as indicated, of C equals B, bars in D – K all equal 1 mm. Drawn by Bobbi Angell.

rounded, scarious lobes about as long as the calyx tube (Fig. 2D – F). The androecium is adnate to the perianth, diverging from the calyx tube about 0.1 mm below the separation of the calyx lobes (Fig. 2F – H). It consists of a shallow filament tube 0.1 – 0.2(– 0.4) mm high and five broad-based, free filaments that taper to the introrse anthers. This perigynous condition of the androecium is otherwise unknown in the Amaranthaceae. Vascularization to the perianth consist of five separate traces each extending directly from the receptacle into one of the calyx lobes (Fig. 2G). As in *Gossypianthus* the androecium contains no vascular tissue. At flowering time the calyx lobes reflex sharply exposing the stigma and anthers that are produced at about the same level. After anthesis the lobes either close or remain basally reflexed with the tips curved upward. Opening and closing of the calyx lobes is controlled by a unique system of fibers that are here designated as the *perianth fibrous system*.The fibrous tissue, consisting of slender fibers 50 – 200 um in length and 9 – 15 um in diameter (Fig 2H), occurs all along the main veins from the base of the tube to the mid-perianth lobes (Fig. 2G – H). Fibers are often thickest at the lobe bases, from where they diverge downward from the veins and form a V- or U-shaped band that extends across the upper tube and connects with adjacent sepal veins (Fig. 2G – H). In some flowers, particularly those from North America, the bands of fibers conform to a U-shape.In others it is more in a V- or Y-shape and short series of fibers extend down the calyx tube from the medial portion of the band (Fig. 2G). In South American plants this basal extension of the perianth fibrous system typically extends well down the calyx tube often to the base, causing the tube to appear 10-veined (Fig. 2H). But the perianth fibrous system is not associated with vascular tissue outside of the initial five sepal traces. The perianth fibrous system is often not readily visible from inside the calyx and may not be well developed at anthesis, but it thickens and becomes more apparent in post-anthesis flowers and can be seen from the outside of the calyx tube if the dense wool is pulled away from the upper calyx tube. This perianth system apparently functions in controlling the opening of the perianth throat at anthesis. As the U- or V-shaped fibrous bands expand they force the calyx traces apart and open the calyx throat. Opening also involves reflexing of calyx lobes partly due to swelling of the inner (adaxial) surface of the veins at the throat. Development of the perianth fibrous system continues during the post-flowering period, and as fruits mature the system closes the perianth throat while the calyx lobes may remain partially reflexed or erect after anthesis. As fruits mature the basal portion of the thin pericarp wall irregularly ruptures and the paired bracteoles and fruit fall as a unit dispersed by the dense pericarp wool.

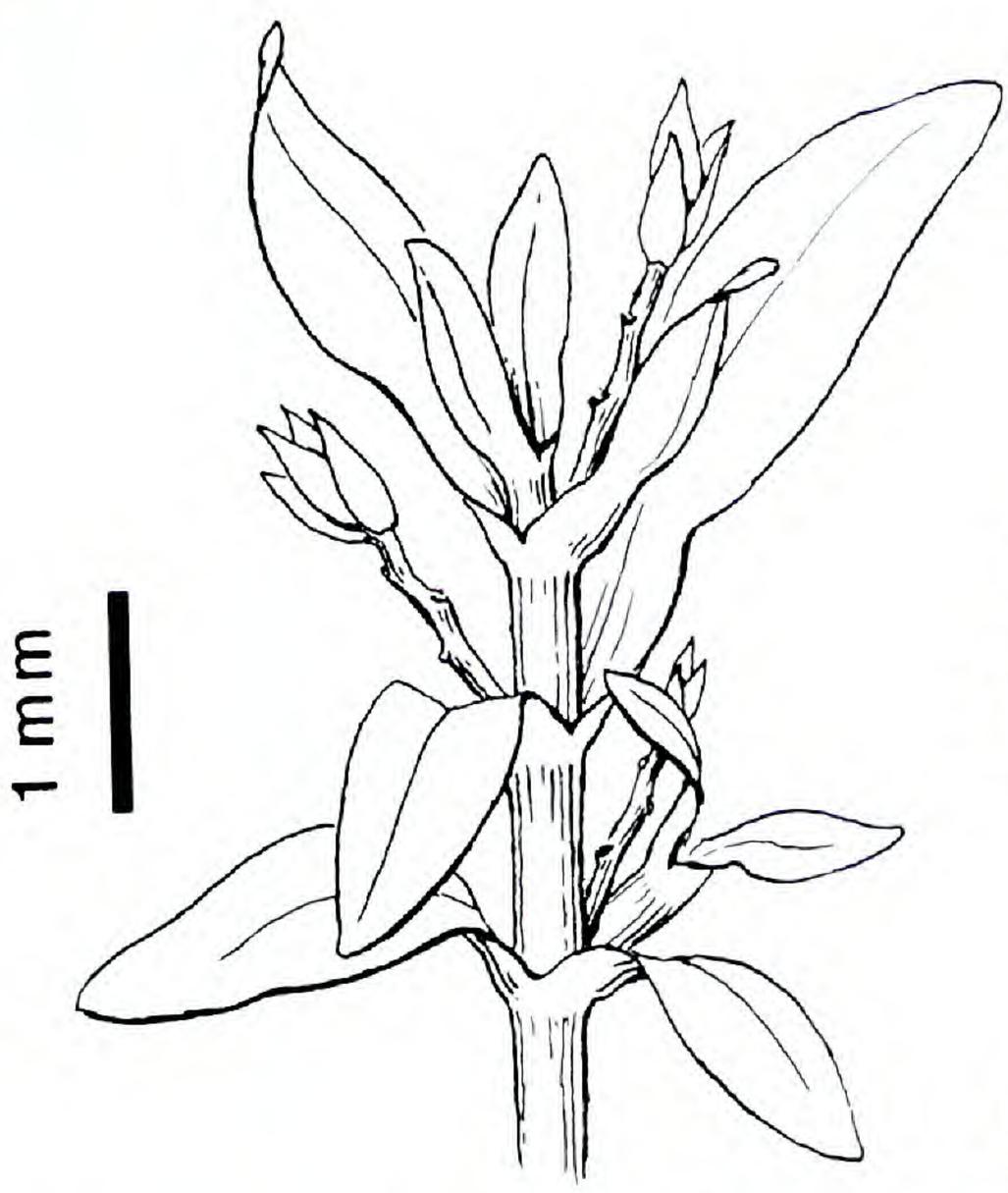

FIG. 3. Arrangements of leaves and flowers on shoots of *Gossypianthus* and *Guilleminea*. A – B *Gossypianthus lanuginosa*. A. Stylized drawing of stem tip showing opposite, unequally sized, basally connate leaves and axillary inflorescences and lateral shoots. (*Pringle 689* GH).B. Diagramatic, 2-dimensional representation of A, showing stem axies as encircled X's, inflorescence axies as solid circles, leaves as crescents, and flowers as small open circles each with 1 outer bract, 2 lateral bractlets. Only 5 flowers are arranged around each inflorescence axis. C – D. *Guilleminea densa*. C. stylized drawing of stem tip similar to A. (*Correll 14026*, LL) D. Diagramatic representation of C, similar to that shown in B. The two genera are basically similar in organography. Scales equal ca. 1 mm. Drawn by Bobbi Angell.

As indicated above, the flower structure of *Guilleminea* differs considerably from that of *Gossypianthus*. These differences have been recognized in more recent treatments of the family (Standley 1917, Schniz 1934) as significant. Mears (1967), however, combined the two genera, recognizing *Gossypianthus* as a subgenus of *Guilleminea* and arguing that *Guilleminea* had been "separated from *Gossypianthus* primarily because of the adnation of the filament tube to the fused calyx." He presented a series of five arguments supporting his congeneric treatment (Mears 1967, p. 138), noting that both genera have filament tubes, and that as the rigid tissue associated with midvein of the calyx tubes decreases, the scarious tissue increases, which he interpreted as transitional between the genera. Much of his argument, however, is confusing and based on a misinterpretation of the flower structure of his *Guilleminea australis*, in which he concludes that the filament tube is actually borne at the base of the calyx lobes (not at the top of the calyx tube as in other species). As such, he feels it represents a transition between the two genera. He illustrates the same in his Fig. 1Ca and to some extent in his Fig. 1Ba. However, adnation of the filament tube to calyx lobes has never been observed in any specimen of *Guilleminea* by me (including the type specimen and other specimens so annotated as *G. australis* by Mears). What he thought was the sinus between the calyx lobes was actually the V- or U-shaped perianth fibrous system in the top of the calyx tube. His interpretation demands that the delicate membranous filament tube pass across the sinuses between the adjacent calyx lobes. The base of the filament tube would then be attached to nothing in the sinus region between the calyx lobes—a quite untenable situation. Thus, Mears (1967) failed to present accurate or meaningful data indicating transitions between the two genera and his arguments are largely based on misinterpretations of the actual structures.

One could argue for a congeneric relationship by maintaining that the shared similarities of general habit, leaf, bract, vegetative vestiture, filament tube, absence of pseudostaminodia, ovary-ovule characters, outer perianth vestiture etc. are shared primitive characteristics (many of these also are shared with other genera in the Gomphreneae) and that the distinctive floral characters of *Guilleminea* are merely a series of uniquely specialized features involving a shift in the intercalary meristems from the base of the calyx lobes to the base of the calyx tube with concomitant development of a perianth fibrous system to control opening of the calyx at anthesis and a reduction in vascularization from three to one trace per lobe as the calyx became more scarious. Although development of the unique calyx features of *Guilleminea* may have involved these types of morphogenetic alterations, the end product represented in the derived *Guilleminea* flower

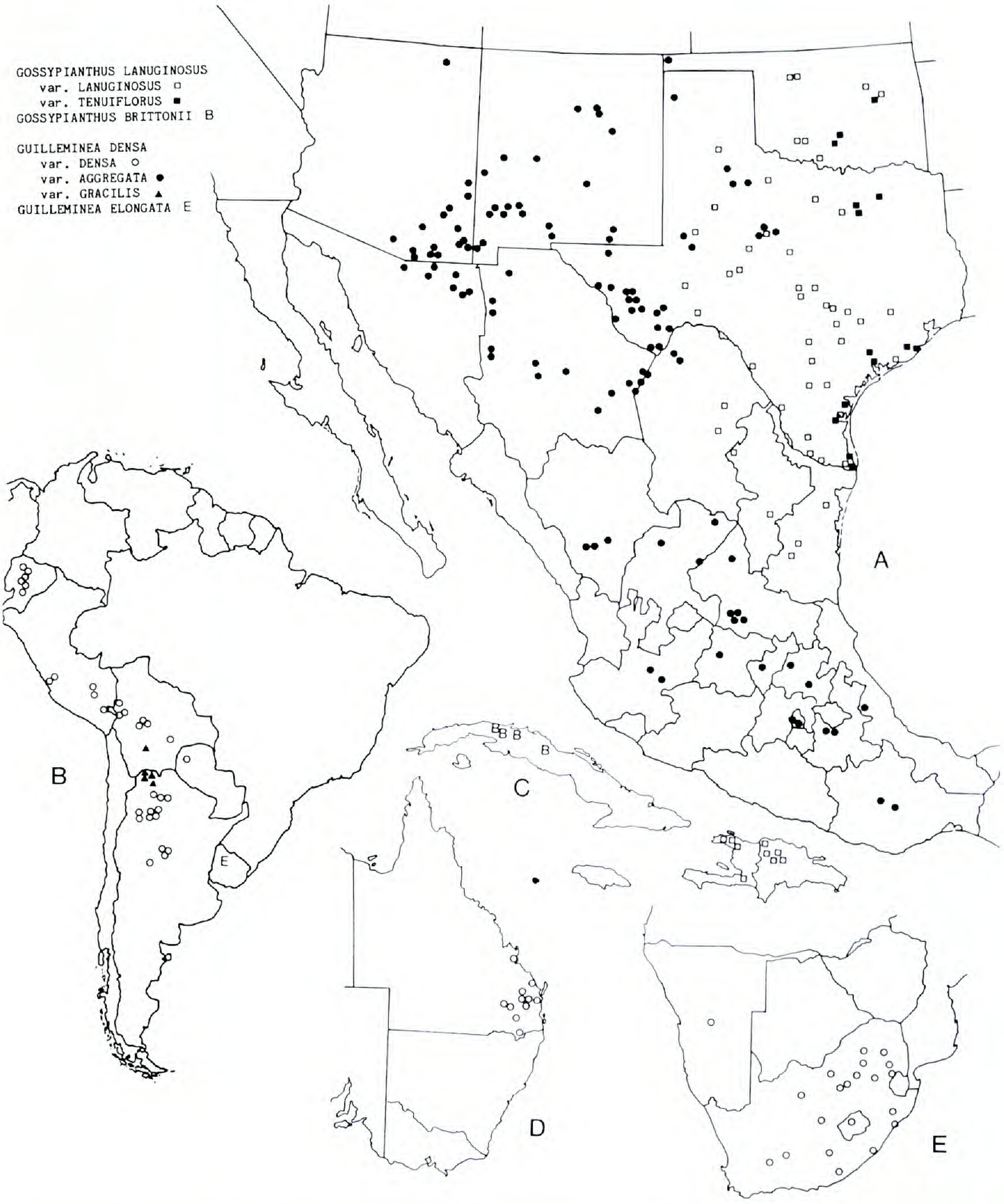

FIG. 4. Distribution of taxa of *Gossypianthus* and *Guilleminea* in A. North America, B. South America, C. Cuba and Hispaniola (Haiti and the Dominican Republic), D. eastern Australia, and E. Southern Africa.

structure are fundamentally very different from those of *Gossypianthus*, *Achyranthes*, *Pfaffia* and *Alternanthera*. J.D. Hooker noted in Bentham and Hooker (1880 p. 22) that overall, the genera within the Gomphreneae are difficult to delimit with certainty. That is certainly not the case with *Guilleminea*.

Mears himself has conceded that problems exist with his submergence of *Gossypianthus* and *Guilleminea*. As Robertson (1981) noted *Gossypianthus* was treated as distinct from *Guilleminea* in Kartez and Kartez's (1980) checklist of Amaranthaceae that was reviewed by Mears. This postdates my early correspondence with Mears about his 1967 treatment.

Regarding relationships within the Gomphreneae, *Gossypianthus* appears derived from *Alternanthera*. Many of the characteristics found in *Gossypianthus* are also found in various species of *Alternanthera*, including procumbent habit, opposite leaves of unequal size with Kranz internal anatomy, axillary spikes, scarious bracts-bracteoles, separate 3-veined, strongly woolly sepals of unequal size (the two smaller, more keeled ones containing the ovary margins), and stamens with a basal filament tube. But in all species of *Alternanthera*, stigmas are spheroidal and papillate (not bilobed), and most species have pseudostaminodia, quite thickened sepals, sometimes thickened bracts, and aculeate-barbed uniseriate hairs on sepals.

Guilleminea shares some characters with *Tidestromia* (1-veined sepals) and with *Froelichia* (sepals united at the base), but as with *Tidestromia* and *Froelichia* it is a clearly defined offshoot from the core of the Gomphreneae.

Taxonomic Treatment

The two genera can be separated by the following key.

Calyx of 5 separate sepals, each oblong-lanceolate to narrowly lanceolate, 3-veined, usually green medially with narrow membranous margins (best observed by pulling off the dense exterior calyx hairs with forceps); filaments free from ovary and calyx; filament tube borne at base of calyx and surrounding ovary; radical leaves persisting at flowering. (Fig. 1) . . 1. *Gossypianthus*

Calyx with basal campanulate tube about as long as the 5 lobes; free calyx lobes each 1-veined with broad membranous margins; filament tube borne near inside top of calyx tube; radical leaves usually absent at flowering. (Fig. 2) . . . . . 2. *Guilleminea*

GOSSYPIANTHUS Hook., Icon. Pl. 3:t. 251. 1840. *Guilleminea* Kunth in H.B.K. subgen. *Gossypianthus* (Hook.) Mears, Sida 3:145. 1967. Type species: *Gossypianthus rigidiflorus* Hook.

Procumbent to decumbent, pilose, sericeous to woolly-villous, perennial herbs from a simple to much-branched, taprooted caudex. Radical leaves linear-oblanceolate, elliptical to spatulate, entire, tapering to a broadly winged, often achlorophyllous, basally sheathing petiole, variously pilose-setose throughout or more softly sericeous-woolly with more slender hairs beneath, often glabrate above, or glabrous throughout, persistent; cauline leaves opposite-subopposite, the pair subequal and oriented about 120

degrees apart, often crowded and progressively reduced in size along distal shoots and in proliferating lateral shoots that develop in alternating directions at nodes; cauline leaf blades ovate to oblong-elliptical, entire, sometimes revolute when dried, with midvein strongly impressed above, raised beneath, with Kranz internal anatomy, glabrous to variously pilose-villous, glabrate, tapering to a broad, often achlorophyllous, basally sheathing petiole at base; membranous wings of opposite leaves connate around nodes. Flowers congested in alternate axils, borne in groups of 1 – 20 or more in globose to cylindrical spikes; spike rachis zig-zagged, strongly sericeous at protruding nodes; bracts solitary, concavo-convex, conduplicate, white, ovate, membranous throughout, glabrous; bractlets 2, similar to bracts in texture, color, shape, but more conduplicate, slightly longer, but shorter than calyx, both bracts and bracteoles tending to fall with fruit; calyces of 5 separate, 3-veined, unequal sepals that reflex at anthesis and close after anthesis, outer 3 sepals broader, oblong-lanceolate, acute, flattened, thickened and usually green medially with scarious margins; inner 2 sepals slightly shorter, narrower, with basal two-thirds more concave and fitting over edges of ovary, thickened, green medially with narrower scarious margins, distal one-third more flattened, green or scarious; all sepals densely woolly villous with crinkled to straight hairs on outside surfaces, becoming rather chartaceous with age, with mid or all 3 veins becoming prominently raised at least near base; stamens 5, free from sepals and ovary, opposite sepals, monadelphous; filaments white, membranous, without vascular tissue, united at base into a short tube; separate filaments broadly dilated, flattened at base; anthers oblong, light yellow, 1-thecal, 2-locular, introrse; ovary superior, compressed, oblong-obovoid, membranous below, with marginal veins weak at base, thickened near tip; style short, broad, bifid distally into two stigmatic surfaces; ovule 1, funiculus extending from a basal placentae to tip of ovule. Fruit utriculate, dehiscing irregularly at or near membranous base; seed 1, compressed ovoid, shiny, smooth, light reddish-brown; embryo peripherial, annular; cotyledons 2, incumbent, radicle erect; perisperm central, translucent.

With two species separable by the following key:

Mature styles (0.1 –)0.2 – 0.3 mm long; lateral stems produced at ground level; Hispaniola, Texas, Oklahoma, Arkansas, and adjacent México. . . . . 1. *G. lanuginosus*

Mature styles 0.5 – 0.9 mm long; lateral stems originating below ground surface; Cuba. . . . . 2. *G. brittonii*

1. Gossypianthus lanuginosus (Poir.) Moq. in A.DC.

Prostrate to decumbent perennial herbs 1 – 7 dm in diameter; stem internodes 0.2 – 2(– 6.5) cm long, 0.4 – 1 mm in diameter, longest at base,

usually reduced in length distally, slightly zig-zagged, yellow, sparsely pilose to strongly woolly-villous with whitish, straight to wavy-crinkled hairs 1 – 3.8 mm long. Basal radical leaves linear-oblanceolate to spatulate, 2 – 9.7 cm long, (1.0 –)2 – 10(– 17) mm wide, acute to obtuse, apiculate at tip, narrowly cuneate above a slender-winged, sheathing petiole 5 – 20 mm long at base; cauline leaf-blades ovate, elliptical-ovate to oblong-ovate, (1.5 –)5 – 18(– 33) mm long, (1 –)2 – 7(– 13) mm wide, glabrous or sparsely to densely pilose to strigose with straight, firm hairs 0.5 – 3 mm long, to glabrate, dull green to yellow-green above, glabrous to more strongly pilose-villous with finer, more wavy, crinkled hairs 0.5 – 3 mm long beneath; petioles winged, sheathing-clasping, (0.5 –)1 – 5 mm long, (0.5 –)1 – 2 mm wide at base. Spikes globose to cylindrical, 1 – 10(– 15) mm long, 5 – 8 mm wide; spike rachis internodes 0.1 – 1.2 mm long; bracts ovate to narrowly ovate, 1 – 2 mm long, 1 – 1.5 mm wide; bracteoles 1.5 – 2.6 mm long, 1 – 1.4 mm wide; calyces 2.4 – 3.5(– 4) mm long; outer larger sepals 2.5 – 4 mm long, 0.6 – 0.8 mm wide, green medially, scarious margins 0.15 – 0.2 mm broad to tip, inner sepals slightly shorter, 2.5 – 3.6 mm long, narrower, 0.4 – 0.5 mm wide; exposed sepal surface densely woolly-villous with straight to wavy hairs 0.5 – 2.0 mm long; stamen filaments 0.6 – 1.1 mm long, basal tube 0.25 – 0.4 mm high; dilated filaments ovate, 0.3 – 0.6 mm long; anthers 0.2 – 0.3 mm long, borne at style height at anthesis, ca two-thirds of fruiting ovary height. Mature ovary 1.4 – 2 mm long, 0.8 – 1.0 mm wide; styles 0.2 – 0.33 mm long; stigmatic lobes 0.1 mm long. Seeds 0.8 – 1.2 mm long, 0.6 – 0.9 mm wide, 0.4 – 0.6 mm thick, reddish brown.

As treated here *Gossypianthus lanuginosus* consists of two varieties, *G. l.* var. *lanuginosus* and var. *tenuiflorus*. Moquin-Tandon (1834) recognized three species in this group (*G. tenuiflorus*, *G. rigidiflorus*, *G. lanuginosus*), as did Standley (1917) [*G. lanuginosus* (including *G. rigidiflorus*), *G. tenuiflorus*, *G. sheldonii*]. Mears (1967) recognized the four taxa as varieties of his *Guilleminea lanuginosa* (vars. *lanuginosa*, *tenuiflora*, *rigidiflora*, and *sheldonii*). I consider only one of these taxa, *tenuiflorus*, to show sufficiently consistent correlated differences to warrant recognition in this treatment. The additional taxa are based on differences in and persistence of leaf and stem vestiture, the size and shape of radical and cauline leaves, and in Standley's treatment, inflorescence shape and length. Most of these characters, however, vary greatly and overlap considerably. To reflect this variation Mears recognized the above taxa as varieties, but his varieties do not have distinct geographical ranges as would be expected for typical varieties. It is critical, in this regard, to know how much of the variability

expressed is due merely to environmental conditions (moisture availability, shading) vs. how much is under strict genetic control. The floral characteristics are basically identical in all taxa recognized here though differences in inflorescence size and shape do occur. The two varieties recognized here can be separated by the following key:

Radical leaves oblong-oblanceolate to spatulate; cauline leaves ovate to oblong-ovate; leaves pilose to sericeous beneath, pilose to glabrate above. . . . . 1a. *G. lanuginosus* var. *lanuginosus*

Radical leaves linear to linear-oblanceolate; cauline leaves oblong-elliptical to oblong; leaves glabrous throughout or with few scattered marginal hairs near base. . . . . 1b. *G. lanuginosus* var. *tenuiflorus*

1a. GOSSYPIANTHUS LANUGINOSUS (Poir.) Moq. in A.DC. var. LANUGINOSUS, Prodromus 13(2):337. 1849. TYPE: Saint Dominque (Dominican Republic), (HOLOTYPE: P-Herb. Desfontaines *fide* Poir.). *Paronychia lanuginosia*, Poir. in Lam., Encycl. Meth. suppl. 4:303. 1816; *Illecebrum lanuginosum* Poir. ex Moq. in A.DC., Prodromus 13(2):337. 1849, *nom. illegit.*; *Guilleminea lanuginosa* (Poir.) Hook. f. in Benth. & Hook., Gen. Pl. 3:37. 1880.

Illecebrum lanatum Moq., *loc. cit., nom. illegit.* [in hort. Paris].
Celosia piloselloides Poit. ex Moq., *loc. cit., nom. illegit.* [in herb.].
Achyranthes piloselloides Poit. ex Moq., *loc. cit., nom. illegit.* [in herb.].
Gossypianthus rigidiflorus J.W. Hook., Icon. Pl. 3:t. 251. 1840. TYPE: UNITED STATES. TEXAS, *Drummond 262* (HOLOTYPE: K!; ISOTYPES: GH!, NY!); *Guilleminea lanuginosa* var. *rigidiflora* (Hook.) Mears, Sida 3:149. 1967.
Gossypianthus lanuginosus var. *sheldonii* Uline & Bray, Bot. Gaz. 20:342. 1895. TYPE: UNITED STATES. OKLAHOMA, (Indian Territory) near Cash (Cache) Creek, Jul 1891, *C.S. Sheldon 170* (HOLOTYPE: US, PHOTOS NY-2!; ISOTYPE: NY!). *Gossypianthus sheldonii* (Uline & Bray) Small, Fl. SE. U.S., (ed. 1), p. 394. 1903. *Guilleminea lanuginosa* var. *sheldonii* (Uline & Bray) Mears, Sida 3:149. 1967.

Lower internodes elongate, upper internodes usually shorter with leaves and flowers variously crowded. Radical leaves oblong-oblanceolate, oblanceolate to spatulate, (16−)35−60(−85) mm long, (3.5−)5−12(−17) mm long, acute to obtuse, apiculate at tip, pilose-setose with ascending, white, rather coarse hairs 0.5−3 mm long, variably glabrate above, more densely pilose to pilose-sericeous with softer, more slender, denser, ascending hairs beneath; cauline leaves ovate, to oblong-ovate, or obovate, (1.5−)5−18(−33) mm long, (1.5−)3−7(−13) mm wide, acute at tip, vestitured as radical leaves but hairs tending to be more persistent; flowers 2.4−4 mm long, outer mature sepals usually developing three prominently raised veins on abaxial surfaces (Fig. 1, 3A).

The type of the species was collected in Santo Domingo (Dominican Republic). Both Standley (1917) and Mears (1967) considered their taxa *lanuginosus* to also occur in Texas and adjacent mainland areas. Hispaniola

specimens are not densely pilose, but hairs persist on both leaf surfaces and they also tend to have smaller radical and cauline leaves, but not as short as stated by Mears (1967). Mears reported radical leaves 10 – 25 mm long and cauline leaves 5 – 8 mm long, 3 – 4 mm wide from Hispaniola specimens, however, a study of 20 specimens from Hispaniola showed longest radical leaves average 32 mm (range 10 – 51 mm), and one specimen from Haiti had cauline leaves 6 – 14 mm long. Reliance on leaf size characteristics to distinguish these taxa, as done by Mears (1967), does not work. The leaf sizes present in available specimens from Hispaniola fall well within the variation found in leaf sizes in mainland specimens. Variation also occurs in leaf vestiture, with some Hispaniola specimens being nearly glabrate, but most are sparsely pilose above, densely pilose-sericeous beneath.

Taxon *rigidiflorus*, described by Hooker (1840) as *Gossypianthus rigidiflorus*, was based on a Drummond collection from Texas. The taxon was included in *Gossypianthus lanuginosus* by Standley but recognized as the most common mainland variety of *Guilleminea lanuginosa* by Mears (1967). It was characterized by Mears by its rather dense pilose stems and lower leaf surfaces with upper leaf surfaces ranging from pilose to variously glabrate. Leaves are generally larger than those in taxon *lanuginosa*, but smaller than those in taxon *sheldonii* with radical leaves being spatulate-oblanceolate, 16 – 60 mm long, 5 – 10 mm wide, and most cauline leaves are 7 – 18 mm long, 3 – 13 mm wide. The taxon exhibits considerable variation, and as Mears noted it intergrades with all other varieties. It is not recognized nomenclaturally in this treatment.

Taxon *sheldonii* described as *Gossypianthus lanuginosa* var. *sheldonii* by Uline and Bray (1895) from an Oklahoma specimen, was recognized as a distinct species by Standley (1917) and as a variety by Mears (1967). It basically includes coarse, large-leaved, densely pilose-sericeous, robust specimens with oblanceolate radical leaves 30 – 85 mm long, and 6 – 12 mm wide and large, spatulate to ovate cauline leaves to 15 – 20 mm long, and 8 – 10 mm wide that are densely aggregated on generally thicker stems. Mears noted the taxon is rare and suggested that it may be merely a large form of taxon *rigidiflora*; with this I agree. It appears merely to represent larger plants with a denser vestiture at one end of a wide range of morphological variation. Where to draw the line between this taxon and specimens referable to taxon *rigidiflorus* would be an arbitrary decision. Both taxa occur in Oklahoma. It is also not recognized nomenclaturally in this treatment.

Gossypianthus lanuginosa var. lanuginosa then is considered a highly variable taxon. It is known from sandy, sandy-loams or limestone-derived clays, caliche hills mostly in open, generally dry, often waste areas from

near sea level to 1500 m from Oklahoma through Texas south into western Coahuila, Nuevo León, Tamaulipas in México and in Haiti and Dominican Republic (Fig. 4A, C).

Representative specimens: UNITED STATES. **Oklahoma**: **Comanche Co.**: Fort Sill, 14 Jun 1916, *Clemens 11564* (GH). **Jefferson Co.**: 8 mi n Waurika, 24 Jul 1948, *Waterfall 8382* (GH). **Major Co.**: 3 mi w Orienta, 20 Aug 1948, *Waterfall 3595* (TEX). **Muskogee Co.**: near Muskogee, 6 Aug 1936; *Osborn 1335R* (US). **Texas**: **Atascosa Co.**: Pleasanton, 16 May 1916, *Palmer 9770* (US). **Briscoe Co.**: 9 – 12 mi n Turkey, 9 Jul 1973, *Higgins 7619* (NY). **Brown Co.**: Brownwood, 2 Oct 1965, *McCart 9278* (LL, TEX). **Burnett Co.**: Bluffton, Oct 1879, *Palmer 1143* (GH): Cameron Co.: Loma de la Jauja, Jun 1952, *Johnston 79-7* (TEX). **Duval Co.**: 1 mi s Benavides, 25 Jun 1962, *Correll & Johnston 25514* (LL). **Irion Co.**: 8 mi sw Mertzon, 14 Sep 1961, *Correll & Johnston 24614* (GH, LL). **Jim Hogg Co.**: 30 mi s Hebbronville, 15 Jun 1928, *Tharp s.n.* (TEX). **Knox Co.**: Brown Ranch on Wichita River, 22 Aug 1972, *Higgins 6155* (NY). **Llano Co.**: Llano, 14 May 1899, *Bray 328* (TEX). **Martin Co.**: 18 mi n Midland, 12 Jul 1977, *Higgins 10313* (NY). **Matagorda Co.**: 2.5 mi w Gulf, 10 Oct 1934, *Cory 11531* (GH). **Maverick Co.**: 15 mi e Eagle Pass, *Bray 30* (TEX). **McMullen Co.**: 20 mi sw Tilden, 31 May 1949, *Rogers & Webster 6810* (TEX). **Pecos Co.**: Mesquite Valley, 15 Jul 1943, *Tharp 43-550* (TEX). **Starr Co.**: 17.5 mi n Sullivan City, 12 Nov 1940, *Cory 36135* (GH). **Tarrant Co.**: rich woods, 16 Aug 1919, *Ruth 2* (LL). **Taylor Co.**: Clyde, 9 Jul 1941, *Tharp s.n.* (TEX). **Terrell Co.**: 18 mi s Sheffield, 1 – 2 Jul 1949, *Webster 463* (TEX). Travis Co.: Austin, 25 Jul 1939; *Tharp s.n.* (TEX).

MÉXICO. **Chihuahua**: Plains near Chihuahua, 22 Aug 1885, *Pringle 689* (GH, LL, NY-2, US). **Coahuila**: 12 mi n Monclova, 22 – 24 Aug 1938, *Johnston 7188* (GH, US). **Tamaulipas**: 20 mi w Reynosa, 28 Feb 1944, *Painter & Barkley 14389* (GH, LL); vic Victoria, 320 m, 1 Feb-9 Apr 1907, *Palmer 74* (GH, NY); 5 mi n San Fernando, 14 Sep 1960, *Crutchfield & Johnston 5498*, (TEX-approaching var. *tenuiflorus*). *Nuevo León*: 8 mi w Linares, 30 Sep 1960, *Crutchfield & Johnston 5834a* (TEX); 3.5 km wnw Rancho La Mesa, 16 Mar 1973, *Johnston et al 10204* (LL).

HAITI. Etang, rd to Thornazian, 13 – 17 May 1920, *Leonard 4231* (NY, US); Port de Paix, rd to Moustique, 16 May 1925, *Ekman 4039* (NY). Dept. l'Artibonite, vic Gros Morne, 235 m, 17 Feb 1926, *Leonard 9852* (NY); w of Cabaret, 16 Jan 1929, *Leonard & Leonard 12077* (US); Jean Rabel Rd, 27 Jan-9 Feb 1929, *Leonard & Leonard 12654* (NY).

DOMINICAN REPUBLIC. Guayubin, 100 m, 13 – 21 Feb 1921, *Abbott 865* (NY): La Herradura, 2 Apr 1950, *Jimenez 1944* (US); nr Rio Yaque del Norte, s of Monte Cristi, 23 – 4 Oct 1946, *Howard & Howard 960*, (NY); La Lava, 25 km nw Santiago, 250 m, 6 May 1968, *Liogier 11199* (NY); 25 mi e Monti Cristi, 50 m, 7 Jun 1969, *Liogier 15612* (NY) (Fig. 4A, D).

1b. Gossypianthus lanuginosus var. **tenuiflorus** (Hook.) Henrickson comb. et stat. nov. *Gossypianthus tenuiflorus* Hook., Icon. Pl. 3:t. 251. 1840. Type: UNITED STATES. Texas, *Drummond 262* (holotype: K!). *Guilleminea lanuginosa* var. *tenuiflora* (Hook.) Mears, Sida 3:147. 1967.

Lower and upper internodes tending to be elongate with clusters leaves and flowers generally widely dispersed. Radical leaves linear to linear-oblanceolate, (18 –)35 – 97 mm long, (2 –)3 – 6.5(– 9)[– 11] mm

wide, acute, glabrous throughout or with few marginal hairs near base; cauline leaves oblong, oblong-elliptical to oblong-oblanceolate, rarely ovate, often obliquely recurved, 10 – 17(– 20) mm long, (1.5 –) 2 – 5(– 8) mm wide, narrowly acute, glabrous or soon glabrate except for occasional basal marginal hairs; flowers (2.5 –)3 – 4 mm long; tending to form into elongate, cylindrical spikes 8 – 13 mm long; outer mature sepals with central vein more prominently raised than lateral veins.

Taxon *tenuiflora* was described as a species by Hooker (1840) from the same Drummond collection (No. 262) that provided the type of taxon *Gossypianthus rigidiflorus*. *Gossypianthus rigidiflorus* was characterized as having sepals with strongly striated ridges (i.e. three prominently raised veins); *G. tenuiflorus* had thin, membranous, non-striate sepals. Hooker (1840) noted that the growth habit of *G. tenuiflorus* "is exactly that of *G. rigidiflorus*, nor can I point out any other characters save the difference in the perianth." So as initially defined by Hooker (1840) *G. tenuiflorus* differed only in the lack of well defined veins in the perianth, but it was vegetatively identical with *G. rigidiflorus*.

Uline and Bray (1895) considered both *G. rigidiflorus* and *G. tenuiflorus* synonymous with *G. lanuginosus*. Moquin-Tandon (1849) apparently saw the original type material and described the distinct vegetative differences between the taxa. Standley (1917), following Moquin-Tandon (1849), recognized *G. tenuiflorus* as vegetatively distinct from his *G. lanuginosus*, having "leaf-blades glabrous or nearly so, the basal ones acute; flowers distinctly spicate, the spikes usually longer than broad." Mears (1967) followed Standley in distinguishing his *Guilleminea lanuginosa* var. *tenuiflora* as having "radical leaves usually 40-90 mm long, often linear; plants large, often with ascending stems; plants often nearly glabrous." Observations on the type material from Kew confirmed the vegetative differences as described by Moquin-Tandon and later authors. The attribute of sepal venation initially stressed by Hooker also occurs, as only the midvein of the three sepal veins becomes prominently thickened with age and this is mostly limited to the lower half of the sepal.

The taxon is distinguished by its narrow, usually glabrous radical leaves. Some intergradation occurs with var. *lanuginosa*; these plants have the general habit of var. *lanuginosa* but glabrous leaves; other plants strongly vestitured like *lanuginosa* have narrower, oblong-elliptical cauline leaves. Intermediate specimens are most common in southmost Texas and adjacent Mexico. *Gossypianthus lanuginosus* var. *tenuifolius* is known from scattered collections from coastal and east Texas from southern Oklahoma and from one indefinite locality in Arkansas (Fig. 4A). It apparently occurs with var. *lanuginosa* through a portion of its range. Such co-occurrence and its

corresponding lack of a discrete geographical range would tend to favor recognition at the species rank, but the the observed intergradation between the two varieties speaks against that.

Representative specimens: UNITED STATES. (The first 4 collections are from Whipple's Exploration for a Railway Route 1853-4) ARKANSAS: Without data, 1853-4, *Bigelow s.n.* (NY). OKLAHOMA: Grand Prairie, 22 Aug, *Bigelow s.n.* (NY): upper Canadian River, *Bigelow s.n.* (US); prairie near Sabine River, Leavenworth (NY); on false Washitaw between Ft Cobb & Ft Arbuckle 1868, *Palmer 282* (NY). Creek Co.: Supulpa, 27 Sep 1894, *Bush 481* (GH, NY-4, US-with some specimens approaching var. *lanuginosa*). **Garvin Co.**: 8 mi w. of Davis, 6 Nov 1944, *Waterfall 5879* (GH, NY). TEXAS: Brazoria Co.: Columbia, 30 Oct. 1899, *Bush 296*, NY, US-2). **Cameron Co.**: Laguna Atascosa Refuge, 21 Sep 1961, *Fleetwood 3809* (TEX); Sacahulste Flats, Jun 1952, *Johnston 79-5* (TEX). **Dallas Co.**: Dallas, Aug, *Reverchon 2379* (GH, NY-3). **Jackson Co.**: Lavacca River, 28 Aug 1941, *Tharp s.n.* (TEX). **Hunt Co.**: Commerce, 1 Jul 1941, *Strandtmann 1* (TEX). **Kleberg Co.**: w Laurles division King Ranch, 17 Sep 1954, *Johnston 541671* (TEX). **Nueces Co.**: nr Corpus Christi, May 1898, *Heller s.n.* (NY); (Fig. 4A).

2. GOSSYPIANTHUS BRITTONII Standl., Contr. U.S. Natl. Herb. 18:92. 1916. TYPE: CUBA., SANTA CLARA, rocky hill in a palm barren, Apr 1912, *N.L. Britton & J.F. Cowell 13318* (HOLOTYPE: NY!; ISOTYPES: GH!, TEX!). *Guilleminea brittonii* (Standl.) Mears, Sida 3:150. 1967.

Gossypianthus jackianus Ekman & Seusseng., Repert. Spec. Nov. Regni Veg. 35:317. 1934. TYPE: CUBA. PROV. MATANZAS, Canasi, in locis siccissimis, May 1923, *E.L. Ekman 16507* (HOLOTYPE: S; ISOTYPE: NY!).

Gossypianthus heterophyllus Ekman & Suesseng., Repert. Spec. Nov. Regni Veg. 35:317. 1934. TYPE: CUBA. PROV. MATANZAS, Ponce, sterile Ortlichkeiten, Aug 1923, *E.L. Ekman 17079* (HOLOTYPE: S; ISOTYPE: TEX!). *Guilleminea brittonii* var. *heterophylla* (Ekman & Suesseng.) Mears., Sida 3:150. 1967.

Procumbent to decumbent perennial herbs 0.5 – 1.5 (perhaps more) dm in diameter, stems mostly branched below ground with several rosettes at ground level; stems with swollen, indurate nodes, with internodes 1 – 12 mm long, 0.3 – 0.8 mm wide, glabrous to sparsely pilose to strongly woolly-villous with white wavy to crinkled hairs 0.5 – 3.0 mm long. Basal radical leaves linear-oblanceolate, oblanceolate, 8 – 15(– 27) mm long, 1 – 3(– 5) mm wide, acute to obtuse at tip, tapering to a broad to slender, flattened achlorophyllous or green petiole 3 – 7(– 14) mm long, 0.6 – 1.2 mm wide at base, with midvein deeply incised above, sparsely, rarely densely pilose-sericeous with hairs 0.3 – 2.0 mm long throughout or only beneath or along expanded midrib and revolute margins beneath; cauline leaves crowded or well spaced, ovate, oblong-elliptical to elliptical, (1 –)2 – 6(– 10) mm long, 1 – 4(– 5) mm wide, obtuse-rounded to acute at tip, rounded to cuneate above a broad, often white-margined petiole 0.4 – 2 mm long at base, at margins entire, often revolute when small,

flattish with a strongly impressed midvein, mostly glabrous above, sparsely to moderately pilose beneath and along lower margins with hairs 0.3 – 1 mm long, with Kranz internal anatomy not conspicuous when leaves dry. Flowers in groups of 3 – 15(– 30) in small spicate glomerules 1 – 5 mm long, 3 – 6 mm wide; bracts and bractlets ovate, concavo-convex, 1.2 – 2.0 mm long, 1.1 – 1.4 mm wide, obtuse to acute at tip, often becoming erose-margined; sepals obscurely 3-veined, of unequal size, outer three sepals larger, 1.9 – 2.6 mm long, 0.7 – 1.2 mm wide, inner two sepals slightly shorter, 0.4 – 0.8 mm wide, more concave at base, exposed sepals surface strongly villous with silky hairs 0.8 – 2.5 mm long; stamen filaments 1.0 – 1.4 mm long, basal tube 0.2 – 0.5 mm high above base, separate filaments 0.7 – 1.0 mm long; anthers yellow, (0.3 –)0.5 – 0.7 mm long; styles (0.4 –)0.5 – 1.0 mm long, stigmatic lobes 0.2 – 0.25 mm long. Seeds ca. 1.2 mm long, reddish brown.

Three species have been named from this Cuban complex characterized by longer styles, short filament tubes, longer free filaments, longer anthers, and a tendency for lateral shoots to develop from underground rootstocks. Each of these three named taxa have certain unique minor characteristics, but as only eight collections were available for study, it has been difficult to determine the significance of these differences.

Only three specimens of *Gossypianthus brittonii*, all type specimens, were available for study. In this single collection plants developed from an evidently buried rootstock; radical leaves were mostly small, but some were to 26 mm long, and 4 mm wide; cauline leaves were small, rather (0.2 mm) thick, and strongly impressed-veined above. Inflorescences were short, to 4 mm long, flowers were moderately long with styles 0.7 – 0.9 mm long, and free filaments were 0.8 – 1.1 mm long. But with only one collection available for study it is not possible to determine the range of variation in this taxon.

The three collections of *Gossypianthus jackianus* were all collected in Matauzus provience in Cuba. They are uniform in their leaf characteristics with each having moderately thick (0.2 mm) leaves as in *G. brittonii*, that are villous to mostly glabrate, with midveins strongly impressed above, long villous beneath; their radical leaves are 6 – 23 mm long, 2 – 5 mm wide and have long slender, narrowly winged petioles to 12 mm long. Inflorescences range from 4 – 8 mm long and are many flowered. Flowers are relatively large with styles 0.7 – 0.9 mm long and free filaments are 1.0 – 1.1 long. In most characteristics the taxon seems referable to *G. brittonii*.

Gossypianthus heterophylla, known from four collections, two from Santa Clara and two from Matanzas provinces in Cuba, can be distinguished by

its more erect habit, its thinner (0.1 – 0.16 mm thick), glabrate, mostly longer leaves (the radical 11 – 24 mm long, 1.5 – 4.3 mm wide), and generally smaller flowers with styles 0.5 – 6.5 mm long, free filaments 0.6 – 0.9 mm long.

Mears (1967) recognized two varieties here—placing taxon *heterophylla* as a variety of *brittonii*. He distinguished var. *brittonii* as having radical leaves only 5 – 7 mm long [they actually measure 9 – 15(– 26) mm in length] with a widely winged petiole devoid of chlorophyll. In all plants leaf-blade margins extend down the petiole. When the petioles are short they appear strongly winged. In longer radical leaves, with longer petioles, wings appear relatively narrower, but in some instances may actually be wider in measurement. Mears also noted differences in style length (perhaps an indication of flower size) and inflorescence size. Indeed the flowers of *heterophylla* appear slightly smaller with styles only 0.5 – 6.5 mm long (not 0.7 – 0.9 mm) and with only one collection of *brittonii* available for study it is difficult to determine the variation present in this taxon.

On the basis of the low number of specimens available to me at this time and considering the possibility of environmentally induced variation, it would appear best to recognize only one taxon here until field work and additional collections can indicate the character variation in the three previously described taxa.

Representative specimens: CUBA. **Prov. Santa Clara**: near Mordazo, 29 Dec 1915, *León & Cazanas 5934* (NY); Dist Cienfuegos, Cieneguita(?), 8-10-1895, *Combs 405* (NY). **Prov. Matanyzas**: Ceiba Mocha towards Canasi, 1 – 3 – 1924, *Ekman 18589* (NY); s of San Jose, 4 Jan 1927, *León & Roig 4139* (NY): Cuabal del Espinal, near Canasi, 4 Jan 1927, *León & Roig 12937* (NY); highest part of Cuabales of Canasi, Jan 1927, *León s.n.* (NY) (Fig. 4C).

GUILLEMINA Kunth in H.B.K., Nov. Gen. Sp. 6:40, t.518. 1823.

Guilleminea subgenus *Guilleminea* (Kunth in H.B.K.) Mears, Sida 3:139. 1967. *Brayulinea* Small, Fl. SE U.S. (ed. 1), 394. 1903. TYPE SPECIES: *Illecebrum densum* Willd. in Roem. et Schult.

Procumbent, pilose, sericeous to woolly-villous perennial herbs from simple, slender to napiform taproots; caudex simple, strongly villous. Stems several, spreading, villous to woolly-villous. Rosulate leaves oblong-elliptical to lanceolate, entire, tapering to a broadly winged, usually achlorophyllous, basally sheathing petiole, rarely persisting at flowering; cauline leaves opposite to subopposite, the pair at a node subequal in size and oriented about 120° apart, producing additional pairs of unequal, smaller leaves in axils of largest or of both leaves of the pair, and this system proliferating to form crowded lateral shoots at alterna-

ting sides along stem nodes, these often much congested or remote; cauline leaf blades ovate to lanceolate, entire, acute to obutse, with Kranz internal anatomy, glabrous, dull to yellow green above, white villous to woolly-villous beneath, tapering to a broadly winged, often achlorophyllous, basally sheathing petiole at base, the membranous wings of opposite leaves connate around nodes. Flowers borne at base of opposite leaves, usually bordered by reduced axillary leaf pairs, congested in groups of 3 – 12 in glomerate spikes; rachis zig-zagged, with 2/5 phyllotaxy, thick, strongly sericeous at protruding nodes; bracts solitary, concavo-convex, white, elliptical-ovate, membranous throughout, persistent on inflorescence; bracteoles 2, similar in texture, color, shape, slightly larger, but shorter than calyces, falling with flowers; calyces sessile or pedicellate; calyx tubes campanulate, ca. as long as lobes, membranous except for 5 veins extending from base into calyx lobes, usually developing a distinct perianth fibrous system that extends as V- or U-shaped thickenings between veins near top of calyx tube, these sometimes developing slender basal extensions that continue down calyx tube alternating with veins, tubes densely villous-woolly outside; calyx lobes 5, equal to subequal, ovate to elliptical, acute to rounded at tip, membranous except along midvein, weakly villous outside, spreading at anthesis but usually ascending later; stamens 5, episepalous, monadelphous, borne at upper rim of calyx tube just below lobe sinuses; filaments white, membranous, without vascular tissue, united basally into a short basal tube separate from calyx with broad rounded sinuses, free filaments tapering, about as long as calyx tube; anthers opposite sepals, oblong, oblong-ovate, light yellow, barely exserted at throat, introrse; mature ovary compressed oblong-obovoid, membranous except along marginal veins and in upper one-fifth, tapering to a cylindric bifid style with two stigmatic lobes; ovule 1, funiculus extending from a basal placentae to tip of ovule. Fruit utriculate, dehiscing irregulary at or near membranous base; seed 1, compressed ovoid, shiny, smooth, chestnut brown; embryo peripherial, annular; cotyledons 2, incubment, radicle erect; perisperm central, translucent.

With 2 species separable by the following key:

Calyces sessile or with a woolly pedicel to 0.3 mm long; bracts-bracteoles and membranous sepal tips usually translucent, thin, clear, sometimes whitish; sepals acute to rounded at tips, equal to subequal in width; perianth fibrous system well developed in post-anthesis calyces seen as U- or V-shaped thickenings on outside of calyx tubes below lobes, sometimes with narrow extension continuing down calyx tubes (the dense exterior calyx vestiture must be pulled away to see this); common. . . . . 1. *Guilleminea densa*

Calyces separated from bracts-bractlets by a distinct, woolly pedicel 0.8 – 1 mm long; bracts-bractlets and sepal tips opaque, relatively thick, ivory to

brownish white; sepals rounded at tip with distinctly incurved margins, unequal in width; perianth fibrous system lacking or poorly developed; known only from Uruguay. . . . . 2. *Guilleminea elongata*

1. GUILLEMINEA DENSA (Willd. in Roem. et Schult.) Moq. in A.DC.

Plants 1−8 dm in diameter; stem internodes 0.1−2.5(−5.0) cm long, 0.5−1.5 mm in diameter, shorter distally or not, slightly zigzagged, yellow to reddish, villous to densely woolly-villous with whitish, crinkled hairs 0.4−2(−4) mm long. Basal rosulate leaves oblong-elliptical to lanceolate, (0.8−)2−4 cm long, (1.5)6−9(−13) mm wide, acute at tip, cuneate above a winged petiole (0.3−)8−20 mm long at base, rarely persisting at anthesis, glabrous above, villous beneath; cauline leaves (0.7−)4−15(−28) mm long; leaf blades broadly to narrowly ovate, oblong-ovate, oblong, rhombic, occasionally elliptical to lanceolate, (1−)2−10(−23) mm long, (0.7−)1.2−8(−14) mm wide, acute to obliquely obtuse-apiculate, acuminate at tip, green, glabrous above, villous to densely woolly-villous with white hairs 0.5−3 mm long beneath; petioles (1−)2−4(−7) mm long, 0.7−1.5(−2.2) mm wide, winged, often curved to orient leaves. Flowers borne in groups of 4−12 in clusters of glomerate spikes 2−3(−4) mm long, 3−5 mm wide; rachis nodal hairs 1−1.5 mm long; bracts translucent, thin, elliptical-ovate, 0.6−1.6(−2.6) mm long; bractlets of similar texture, 1.2−2 mm long, 0.6−1 mm wide; pedicels (when present) 0.2−0.3 mm long; calyces 1.7−2.3(−2.8) mm long; calyx tubes 0.8−1.2(−1.5) mm long, translucent, clear membranous except for 5 veins and perianth fibrous system that develops by and after anthesis, densely villous-woolly outside with wavy white hairs 1−3 mm long; calyx lobes 5, equal to subequal, ovate to elliptical, 0.8−1.5 mm long, (0.3−)0.4−0.6(−0.7) mm wide, acute to rounded sometimes with margins infolding at tip, translucent membranous except along midvein, midvein extending only to lower half or nearly to tip, usually achlorophyllous but sometimes with chlorophyll bordering lower midvein, villous at least near bases; staminal filament tube borne at uniform level near top of calyx tube, tube 0.1−0.2(−0.4) mm high, free filaments broadly dilated at base, narrowed above, 0.1−0.2(−0.3) mm long; anthers 0.13−0.25 mm long; mature ovary 1.1−1.4 mm long, to 0.5−0.6 mm wide; bifid terminal style 0.2−0.3 mm long, stigmatic lobes inconspicuous, ca. 0.1 mm long. Seeds 0.8−0.9 mm long, 0.6−0.7 mm wide, shiny, reddish brown.

Guilleminea densa occurs in both North America (Arizona, Oklahoma to southern Mexico) and South America (Colombia to Argentina) and is naturalized in southern Africa and eastern Australia. (Fig. 4). Over its range it exhibits considerable variation in growth habit and some variation

in flower and root structure that allows recognition of three varieties separable by the following key:

A. Taproots napiform, with a turnip-like or expanded segment below the top; calyx lobes mostly oblong-elliptical, oblong-lanceolate, rarely more oblong-ovate to ovate, mostly narrowly acute-acuminate, sometimes obtuse at tips, midveins extending nearly to sepal tip; sepal lobes erect after anthesis; perianth fibrous system present as V- or U-shaped thickenings near throat with slender extensions continuing down calyx tube, mature calyx tubes thus appearing 10-veined (the dense calyx tube vestiture must be pulled away to see this); South America, naturalized in southern Africa and eastern Australia. . . . . 1a. *G. densa* var. *densa*.

AA. Taproots cylindrical; calyx lobes oblong-ovate, oblong-obovate, oblong-elliptical, broadly acute, obtuse to rounded, sometimes narrowly acute at tips, midveins extending about one-half to two-thirds way to lobe tips; perianth fibrous system developing as V- or U-shaped thickenings near tube throat, the downward slender extensions not present or very short and not extending to calyx tube base, rarely present only between 2 sepals (the dense calyx tube vestiture must be pulled away to see this); North America, northern Argentina, adjacent Bolivia.

B. Plants 10 − 80 cm in diameter; leaves variable, mostly 4 − 15(− 28) mm long, leaf blades 2 − 10(− 23) mm long, 2 − 8(− 14) mm wide; North America. . . . . 1b. *G. densa* var. *aggregata*.

BB. Plants to 10 cm in diameter; leaves small, 2.5 − 9 mm long, leaf blades 1.3 − 7.5 mm long, (0.7 −)1.5 − 3(− 4) mm wide; high elevations in extreme n. Argentina (Dpto. Jujuy) and adjacent Bolivia. . . . . 1c. *G. densa* var. *gracilis*.

1a. GUILLEMINEA DENSA (WILLD. IN ROEM. ET SCHULT.) MOQ. VAR. DENSA in A.DC., Prod. 13(2):338. 1849. *Illecebrum densum* Willd. in Roem. et Schult., Syst. Veg. 5:517. 1818. TYPE: ECUADOR, Quito, *Humboldt and Bonpland 2220*. [HOLOTYPE: B-HERB. WILLD.; ISOTYPES: P-Herb. Humb. (Microfiche!, photos GH!, NY!), P (fragment seen!)]. *Brayulinia densa* (Willd. in Roem. et Schult.) Small, Fl. SE U.S. (ed. 1), 394. 1903.

Guilleminea illecebroides Kunth in H.B.K., Nov. Gen. et Sp. Pl. 6:42. 1824. TYPE: ECUADOR, Quiti (Quito), 1490 hex., *Humboldt and Bonpland 2220* [HOLOTYPE: P-Herb. Humb., microfiche!, photos GH!, NY!, (also an isotype of *I. densum* Willd.); ISOTYPES: P (fragment seen!), B-Herb. Willd.]. *Guilleminea illecebrum* Spreng., Syst. Veg 4(2):103. 1827.

Guilleminea densa var. *alsinaefolia* Moq. in A.DC., Prod. 13(2):338. 1849. *Illecebrum alsinaefolium* Pavon, in herb. (*nom. nudum*) *loc. cit.*

Achyranthes conferta Ruiz in Mart., Fl. Bras. 5(1):223. 1840. *pro. syn.* in Herb. Lambert. *nom. nudum*.

Gossypianthus australis Griseb., Abh. Koenigl. Ges. Wiss. Goettingen. 19:83. 1874. TYPE: ARGENTINA, Haufig auf sandigen sterilen boden bie Ascochinga, Apr 1871, *P.G. Lorentz 384* [LECTOTYPE HERE DESIGNATED: GOET (photo and fragment seen!)]. *Guilleminea australis* (Griseb.) Hook. f. in Benth. and Hook., Gen. Pl. 3:37. 1880. *Brayulinea australis* (Griseb.) Schniz in Engler and Prantl, Nat. Pflanz. (ed. 2). 16c:65. 1934.

Taproots napiform with a distinct thickening 1 – 2.5 cm wide, 2.5 – 6 cm long below caudex, the taproots slender below this thickening; calyx lobes oblong-elliptical, oblong-lanceolate, narrowly acute to acuminate or obtuse with upper margins often incurved around tip, 0.3 – 0.5(– 0.6) mm wide with midvein usually extending to or nearly to sepal tip, erect; perianth fibrous system well developed near calyx tube throats as V- or U-shaped thickenings (as seen from outside in mature, post-anthesis flowers after dense woolly vestiture is pulled away) with lower vertical extensions well developed, extending to or nearly to base of calyx tube alternating with sepal traces, the calyx tubes appearing 10 veined.

Guilleminea densa var. *densa* as considered here is widespread in South America, naturalized in southern Africa, and Queensland, Australia, but does not occur in North America (Fig. 4). The two widespread varieties of *G. densa* recognized here are equally variable vegetatively but differ in root shape and in mature calyx structure as indicated in the key and varietal descriptions. In most South American specimens the calyx lobes are narrowly acute to acuminate (rarely obtuse—see discussion on var. *gracilis* below) with the midvein extending to or nearly (three-fourths way) to the sepal tips. Often the scarious margins inroll around the tip accentuating the narrowness of the tips. These slender, erect sepal tips can usually be seen extending from the wool-covered calyx tubes. Also the distinctive perianth fibrous system typically develops basal extensions down the calyx tube between the calyx lobe traces making the calyx tubes appear to have 10 traces, 5 sepal traces opposite the sepals alternating with these fibrous thickening extensions. As noted above this perianth thickening system may not be well developed at or shortly after anthesis. This set of characteristics occurs in most South American specimens examined to the point I was able to separate South American from North American specimens from mixed stacks in blind tests with an accuracy exceeding 90 percent by looking at the sepal tips or when this was uncertain by looking for perianth fibrous system basal extensions. But, it must be indicated that there is a certain amount of variation in sepal structure and midvein development in both North and South American collections.

The type of *Guilleminea densa* var. *densa* (based on *Illecebrum densum* Willd. ex Roem. et Schult.) was collected by Humboldt and Bonpland near Quito, Ecuador. The illustration accompanying their original description shows a plant with erect, narrow sepals with veins extending to the sepal tips. No fibrous thickening system was shown. In sepal characteristics the type is clearly comparable to other South American, not North American, collections. Mears (1967), however, erroneously considered the type collection to be similar to the North American collections in spite of

this available information and considered var. *densa* to occur in North America as well as in Ecuador and Bolivia. Mears separated his var. *densa* on the basis of whether the calyx lobes were rotate, that is, reflexed at the base (var. *densa*) or completely erect (his var. *gracilis*) after anthesis and whether the sepal vein extended less than halfway (var. *densa*) or more than half way (var. *gracilis*) to the sepal tip. The illustration accompanying the type description clearly shows a plant typical of specimens throughout South America. Observations on fragment of an isotype of the Humboldt and Bonpland collection confirms that the midvein extends nearly to the tip of the narrow sepal lobes and that the calyces indeed do have a well developed perianth thickening system with basal extensions running down the calyx tubes as is characteristic of most South American specimens.

Guilleminea australis was described by Grisebach (1847) from specimens from central Argentina as a *Gossypianthus*. Its original description showed several unusual features: 1) 5 stamens alternating with 5 distinct staminodia; 2) ovules with a basal funiculus; and 3) bilobed bracts. However, in all specimens of *Guilleminea* examined, no staminodia have been observed (if one spreads out the calyx tube for observation, the filament tubes sometime split vertically and the margins point upwards, appearing like staminodia), the funiculus always extends from the basal placenta to the top of the inverted ovule, and bilobed bracts are caused by flattening of the normally cupped bracts, causing them to tear apically. Grisebach did, however, diagram the perianth thickening system accurately, though he considered it all part of the vascular system. Mears (1967) recognized *Guilleminea australis* as a distinct species separated from *G. densa* by two features: 1) a filament tube 0.5 mm high; and 2) sepal veins associated with chlorophyll and extending nearly the length of the sepal. He also noted that the filament tube was connected above the base to the thickened lower sepal midveins (in his species description) or was borne on the base of the free calyx lobes rather than on the top of the calyx tube (in his introduction) a completely untenable arrangement as noted previously. Observations of specimens annotated by Mears as *G. australis* showed one collection with filament tubes 0.4 mm long (the longest observed in the genus) and others to 0.2 mm long, but the filament tube was adnate to the upper calyx tube as expected. In the lectotype material observed the filament tube is only 0.16 mm long and all other features are as in typical *G. densa* var. *densa* leaving no reason to recognize the taxon at any level.

Guilleminea densa var. *densa* occurs in open sandy, gravely slopes, flats along the Andean Cordillara from southern Colombia to central Argentina from 400 to 2700(−3200) m (Fig. 4B) and is also introduced in Queensland, Australia and southern Africa (Fig. 4D−E). Flowering occurs year

around at lower elevations but only in summer-fall at higher elevations.

Representative specimens: COLOMBIA: Puerto Guaitera, Lehmann B-802. ECUADOR: **Prov. Chimborazo**, Riobamba, 2800 m, 9 May 1939, *Asplund 5908* (NY). **Prov. Pichincha**, 25 km nne of Quito, 2460 m, 17 Jan 1945, *Fosberg 22539* (US). **Prov. Imbabura**, n of Ibarra, Nov 1952, *Fagerlind & Wibom 1352* (NY). **Prov. Tungurahua**, Ambato, Dec 1918, *Pachono 91* (GH, NY, US). *PERU*: **Dpto. Junín**, Tarma, 3200 m, 20–22 Apr 1929, *Killip & Smith 21830* (NY). **Prov. Urumbaba**, Vilcanota Valley, Apr 1926, *Herrera 1071* (US). **Prov. Lima**, Matucana, 8000 ft, 14–18 Mar 1923, *MacBride 2924* (GH, NY). BOLIVIA: **Prov. Cochabamba**, Cochabamba 2700 m, 16 Jan 1975, *Graf 502* (NY). **Prov. La PaZ**, Sorita, 10,000 ft, Feb 1886, *Rusby 1513* (NY-4 sheets). **Prov. Santa CruZ**, Cabezas, Playa de Rio Grande, *Peredo s.n.* (NY). ARGENTINA: **Prov. Jujuy**, Dpto. Capitál, e branch of Rio de Reyes, 4 Oct 1938, *Eyerdam & Beetle 22396* (GH). **Prov. Salta**, San Andres, 1800 m, 25 Mar 1945, *Pierotti 1023* (A, NY). **Prov. Tucuman**, Dpto. Capitál, Barranca Colorado, 550 m, Jul 1920, *Venturi 854* (GH, TEX); Dpto. Chichigasta, Cochuna, 4 Mar 1941, *O'Donell 17455* (GH). **Prov. Catamarca**; Indalgala, 2 Feb 1914, *Jorgensen 1677* (NY, TEX). **Prov. Cordoba**, Cordoba, Dec. 1891, *Kuntze s.n.* (NY). **Prov. San Luis**, Candelaria, *Miers 1120* (US). AUSTRALIA: **Queensland**, Emu Park, 19 Feb 1980, *Stanley 648* (BRI); Miles, Morilla Street, 10 Mar 1964, *Clement s.n.* (BRI); Proston, 27 Dec 1956, *Hintz s.n.* (BRI); Gympie, 11 Nov 1933, *White 9614*, (BRI); Bargara near Bundaberg, 14 Nov 1978, *Stanley 78151* (BRI); Ballandean, Stanthorpe Shire, 24 May 1961, *Taylor s.n.* (BRI). SOUTH AFRICA: **Transvaal**, Pretoria, 11 Mar 1943, *Mogg 17018* (NY); Nelspruit, 3 Jun 1978, *West 1123* (PRE). **Cape Provience**, Seven Fountains, eastern Cape, 1200 ft, 10 Jan 1978, *Bayliss 8430* (NY, US, PRE). **Natal**, Tongaat, 23 May 1965, *Strey 5773* (PRE). **Orange Free State**, Parys, Apr 1933, *Oberbeyer 31667* (PRE). **Lesotho**, Roma, Mar 1977, *Schmitz 7336* (PRE). SOUTHWEST AFRICA: **Distr. Windhoek**, farm Schoengelegem, 2000 m, 23 Mar 1961, *Seydel 2613* (NY) (Fig. 4B,D,E). (Not all specimens cited from Australia and Africa were seen by the author—only locality data was seen from BRI and PRE).

1b. Guilleminea densa var. aggregata Uline & Bray, Bot. Gaz. (Crawfordsville) 20:343 1895. Type: MÉXICO, Jalisco, Guadalajara, Jul-Oct 1886, *E. Palmer 471* (lectotype: designated by Mears in herb. NY!; isotype: NY!).

Guilleminea densa var. *humilis* Mears, Sida 3:143. 1967. Type: MÉXICO, Districto Federál, Pedregál de San Angél, Aug 1927, *E. Lyonnet 107* (holotype: NY!; isotype: GH!).

Taproots cylindical, 3–11 mm in diameter, not distinctly thickened below caudex; calyx lobes oblong-obovate, oblong-elliptical, oblong-ovate, broadly acute, obtuse to rounded and usually inwardly cupped at tip, (0.3–)0.4–0.6(–0.7) mm wide with midvein usually extending about half way, occasionally three-fourths way to tip, often somewhat reflexed in lower half with tips more erect; perianth fibrous system well developed near calyx tube throat, consisting of V- or U-shaped thickenings (as seen from outside in mature, post-anthesis flowers after dense woolly vestiture removed) with lower vertical extensions absent or much shorter

than tube, rarely with 1 (of 5 potential) vertical extensions running to base of calyx tube, the calyx tube usually 5-veined; North American (Fig. 2, 3B).

When recognizing the North American material at the variety level the available eipthet at that rank is var. *aggregata*. *Guilleminea densa* var. *aggregata* was initially characterized by its distinctive growth habit consisting of rather coarse plants with long, often thick, primary stem internodes bearing at each node of the main branches a pair of large leaves and large, tightly congested aggregations of smaller leaves and flowers. The entire plant appears like a series of large glomerules of leaves and flowers separated by long internodes. Mears noted the presence of many intermediates between this taxon and var. *densa* and the lack of a distinct geographical range in his var. *aggregata*. Mears, however, stated that flowers of var. *aggregata* were distinctly longer (1.8 – 2.2 mm total length) than those of both vars. *densa* and *gracilis* (under 1.5 mm total length) and that the taxon was recognizable on this basis. This is unfortunately not correct. A brief survey showed that total calyx length of var. *aggregata* as measured from dried specimens averaged 2.07 mm (range 1.7 – 2.8 mm, n = 19) while those of other North American specimens averaged 2.16 mm long (range 1.8 – 2.6 mm, n = 21). This taxon is then only distinguishable by its distinctive growth habit. Interestingly the exact same growth habit occurs frequently in South American collections, but they were not distinguished nomenclaturally by Mears. As the taxon shows no distinct geographic range and has no qualitative or quantitative differences other than elongate internodes, and as numerous intermediate specimens exist, there is no defensible reason to formally recognize this taxon as distinct from other North American material. The name *aggregata*, however, is the one available at the rank of variety for the entire North American taxon as distinguished from the South American var. *densa* on the basis of calyx and root features as indicated in the key and descriptions above.

Guillemina densa var. *humilis* Mears was likewise erected to distinguish plants with a more congested, mat-like growth habit in which the tight clusters of flowers and small leaves are themselves crowded together. Leaves are commensurately reduced and their achlorophyllous petioles are often as wide as the leaf blades. The flowers show no quantitative or qualitative differences from other North American collections. Specimens referable to this taxon are known from rocky habitats in México D.F. and Hidalgo, and several South American collections have similar growth habits (including the type collection of *G. densa* var. *densa*). The taxon appears to merely represent congested individuals occurring on dry microhabitats that continue to proliferate leaves and flowers throughout the dry season. I see no

reason to taxonomically recognize these differences in growth habit.

Guillemenia densa var. *aggregata* occurs in open, dry rocky to sandy, clayey flats, ridges and waste areas from extreme western Oklahoma, western Texas, central New Mexico, southeastern Arizona, continuing south to Oaxaca in México (Fig. 4A) from 1200 – 2600 m elevation. Flowering occurs from May to October.

Representative specimens: UNITED STATES. **ARIZONA**: **Pima Co.**: plains below Baboquivari Canyon, 4 Sep 1931, *Gilman 139* (GH, NY). **Santa Cruz Co. Foothills of Santa Rita Mts,** 7 **May 1881,** *Pringle 329*, (GH, NY, US). **Navajo Co.**: 5 mi n El Capitan, 13 May 1935, *Maguire 11332* (NY). **Greenlee Co.**: 6 mi n Metcalf, 4900 ft, 6 Jun 1935, *Maguire 11809* (NY). **Graham Co.**: Graham Mts., Marijilda Canyon, 2 Jun 1935, *Maguire 12066* (GH, NY). **Cochise Co.**: Ft. Huachuca, 26 Apr 21 May 1890, *Palmer 457* (GH, NY). **NEW MEXICO**: Santa Fe Co.: Vic. Santa Fe, rd to Las Vegas, Sep 1926, *Arsene & Benedict 18061* (US). **San Miguel Co.**: Between Anton Chico and Las Vegas, 1 Oct. 1913, *Rose & Fitch 17646* (NY, US). **Guadalupe Co.**: 6.5 mi n Santa Rosa, 7 Jul 1974, *Higgins 8964* (NY). **Catron Co.**: San Francisco Mts., Cottonwood Campground, 14 Aug 1974, *Pinkava et al. 12496* (NY). **Socorro Co.**: Magdalena to Water Canyon, 1990 m, 12 Jul 1924, *Eggleston 20224* (Gh, NY, US). **Grant Co.**: 16 mi nnw Silver City, 25 Sep 1944, *Hershey 3438* (GH). **Sierra Co.**: Kingston, 6800 ft, 10 Sep 1904, *Metcalfe 1328* (GH, NY-2, US). **Dona Ana Co.**: Organ Mts, 5000 ft, 5 Sep 1897, *Wooton 446* (GH, NY, US). **Lincoln Co.**: Gray, 6000 – 6500 ft, Jul 1900, *Earle & Earle s.n.* (NY). **Eddy Co.**: Dark Canyon, Guadalupe Mts., 12 – 20 Aug 1924, *Standley 40665* (US). **OKLAHOMA**: Cimarron Co.: Tesequite Canyon, 18 Aug 1950, *Goodman & Keiting 5343* (GH, NY, TEX). **TEXAS**: Hartley Co.: 5 mi sw Hdqtrs J Ranch, 15 Aug 1939, *Cory 32615* (GH). **Motley Co.**: w edge Matador, 22 Jul 1974, *Stephens 80649* (NY). **Dickens Co.**: 2 mi n Dickens, 28 June 1964, *Rowell 10291* (GH). **King Co.**: 2 mi s Guthrie, 2 Sep 1973, *Stephens 72546* (NY). **Taylor Co.**: Abilene, 20 May 1902, *Tracy 8048* (NY, US). **Callahan Co.**: Clyde, 7/8/41, *Tharp s.n.* (TEX). **Andrews Co.**: 23 mi se Andrews, Sep 1957, *Scudday s.n.* (LL-2). **Midland Co.**: 4 mi s. of Radio tower, Midland, 10 Jun 1959, *LeSassier 204* (TEX). **Culberson Co.**: Guadalupe Mts, 3.5 mi n Pine Springs Camp, 22 Sep 1946; *Whitehouse 17061* (NY). **Hudspeth Co.**: e side Eagle Mts, 6.5 mi s of Hot Wells, 7 Jul 1943, *Waterfall 4951* (GH). **Jeff Davis Co.**: 20 mi sse of Kent, Davis Mts, 31 Jul 1943, *Waterfall 5427* (GH, NY-2, TEX). **Presidio Co.**: Marfa, 1420 m, 17 Sep 1920, *Eggleston 17300* (NY). **Brewster Co.**: Green Gulch, Chisos Mts, 4 Aug 1936, *Sperry 1243* (US).

MEXICO. **Sonora**: Cañón de Bavispe, 12 Aug 1940, *White 3278* (GH). **Chihuahua**: Madera, 2250 m, 27 May – 3Jun 1908, *Palmer 264* (GH, NY, US); vic Chihuahua, 1 – 21 May 1908, *Palmer 196* (GH, NY). **Coahuila**: Sa. Hechiceros, Canon del Indio Felipe, 27 – 29 Sep 1940, *Stewart 48* (GH); Del Carmen Mts, 9 Aug 1936, *Marsh 682* (GH, TEX-2). **Durango**: Otinapa, 25 Jul – 5 Aug 1906, *Palmer 400* (GH, NY, US). **Zacatecas**: Concepción del Oro, 11 – 14 Aug 1904, *Palmer 312* (GH, NY). **San Luis Potosí**: Region San Luis Potosí, 1878, *Parry & Palmer 787* (GH-2, US). **Hidalgo**: Pachuca, 8000 ft, 19 Jul 1935, *Fisher 35244* (GH, NY); 6.7 mi s Zimapan, 4 Jul 1966, *Mears 215* (TEX). **Jalisco**: Guadalajara, Sep 1886, *Palmer 471* (GH). **México**: Temascaltepec, Luvianos, 20 Jun 1934, *Hinton 6197* (GH, NY). **Veracruz**: Perote, 2350 m, 22 Jun 1970, *Ventura 1337* (NY). **Puebla**: vic Puebla, Aug 1907, *Arsene 1554* (US). **Oaxaca**: vic ruins at Mitlan, 21 Jul 1947, *Rowell et al. 17M471* (TEX). (Fig. 4A).

1c. GUILLEMINEA DENSA VAR. GRACILIS (R.E. FR.) MEARS, Sida 3:143. 1967. *Guilleminea gracilis* R.E. Fr., Nov. Acta Reg. Soc. Sci. Upsal. ser. 4, 1(1):153. 1905. TYPE: ARGENTINA. PROV. JUJUY, Abra Pampa in campo arenoso, 3500 m, 30 Dec 1901, *R. E. Fries 972*. [LECTOTYPE: (selected in herb. by Mears in 1976) S!]. *Brayulinea gracilis* (R.E. Fr.) Schniz in Engler and Prantl, Nat. Pflanz. (ed. 2) 16c:65. 1934.

Plants to 10 cm in diameter; taproots cylindrical, 2 − 3(−5) mm in diameter, not thickened below caudex; calyx lobes spreading at anthesis but later erect, oblong-elliptic, oblong-obovate, oblong-ovate, 0.25 − 0.3 (−0.46) mm wide, acute-acuminate to broadly acute-obtuse, midvein thick, prominent, sometimes surrounded with chlorophyll at base, extending to within 0.2 − 0.5 mm of obtuse to acute tips; perianth fibrous system moderately well developed near calyx tube throat, consisting of V- or U-shaped thickenings, vertical basal extensions absent or much shorter than calyx tube; filament tubes 0.1 − 0.15 mm high; from high elevations in northern Argentina (Prov. Jujuy), and adjacent Bolivia.

Guilleminea gracilis was described by R.E. Fries (1905) from elevations of 3000 to 3650 m in alpine areas in northern Argentina near Bolivia and as accepted here the taxon includes only plants from that area. These are diminutive plants to 10 cm in diameter have reduced, narrowly ovate to oblong-obovate, sparsely villous leaves 2.5 − 9 mm long with broad achlorophyllous petioles, and leaf blades 1.3 − 7.5 mm long, (0.7 −) 1.5 − 3(−4) mm wide. Unlike other South American plants of the genus, the taproots are cylindrical (not napiform), and 2 − 3(−5) mm in diameter. Flowers are few in axillary glomerules, relatively short (1.7 − 2.3 mm long); calyx lobes are very variable, with those of some collections being narrowly acute with veins extending nearly to the sepal tip (typical of var. *densa*) while others (including the lectotype specimen) have shorter, more ovate lobes with more obtuse-rounded tips and thicker midveins extending about half way to the tip (as in North American collections). The perianth thickening system is also poorly developed with the V- or U-shaped horizontal system moderately well developed but the lower extensions in the calyx tube poorly developed (as in North American specimens). These are the only South American specimens having cylindrical taproots, obtuse-rounded calyx lobes without veins extending to near the tips, though this last feature is quite variable, and a generally poorly developed perianth fibrous system. In all these characteristics it approaches North American plants. Plants with similar calyx characteristics also occur at high elevations in Peru (in Departmento de Junin) and in some portions of Bolivia, but these are much larger vegetatively, and have napiform roots and are not considered to be taxon *gracilis*. These smaller northern Argen-

tina specimens are recognized as a separate variety as they do not fit well within var. *densa*. Whether these plants have phylogenetic relationships with similar North American plants or have developed these characteristics independently in these high elevational habitats is not known.

Mears (1969) recognized var. *gracilis* for the bulk of South American plants with acute-acuminate sepals, with veins extending nearly to their tips in contrast to his var. *densa*. His interpretation is not at all in agreement with the sepal characters exhibited by the lectotype and clearly illustrated by Fries (1905). All of the specimens referred to here are small and have slender, cylindrical taproots. It could be that these high-elevation specimens are merely young seedlings of the season that do not overwinter and therefore do not develop napiform roots. If this is so the taxon would be scarcely worthy of recognition, but at present, these collections are distinctive and recognizable from the bulk of other South American specimens.

Guillemenia densa var. *gracilis* occurs in sandy open plains, hillsides from 3000 – 3800(–4000) m elevation on extreme northern Argentina and adjacent Bolivia.

Representative specimens: ARGENTINA: Prov. Jujuy, Region de Puna, Dpto. de Santa Catalina, 3650 m, 18 – 20 Jan 1901, *Claren 11473a* (S); Moreno in campo arenoso, 3500 m, 11 Jan 1911, *Fries 786a* (US); Dpto. Humahuaca; Mina El Aguilár, Espinoso del Diablo, 3800 m, 17 Jan 1971, *Ruthsatz V/23*, (NY); Humahuaca, 3120 m, 27 Jan 1972, *Ruthsatz 322/3* (NY); Churqui Aguada, 3230 m, 28 Jan 1972, *Ruthsatz 326/2)* (NY); Dpto. Cochinoca, Abra Pampa, 3550, 8 Apr 1973, *Ruthsatz 523/2* (NY). BOLIVIA: Potosí, 4000 m, 9 Feb 1932, *Carden 108* (GH). (Fig. 4B).

2. GUILLEMINEA ELONGATA MEARS, Sida 3:145. 1967. TYPE: URUGUAY. TACUAREMBO, Tambores, subsicc., 300 m, Feb. 1937, *W.G. Herter 982* (Plantae Uruguayensis no. 1891). [HOLOTYPE: NY!; ISOTYPE: (fragment from holotype) TEX!].

Plants to 1.6 dm in diameter (probably larger); stem internodes 1 – 3(– 14) mm long, closely villous with crinkled hairs to 1 mm long, glabrate. Basal rosulate leaves lanceolate to elliptical, 10 – 18 mm long, 3 – 6.5 mm wide, acute-acuminate at tip, tapering to a broadly winged, tapering, partially achlorophyllous petiole 3 – 6 mm long at base, entire, glabrous with impressed midveins above, glabrous to closely villous beneath, thin (0.6 mm thick), persisting; cauline leaves crowded, (4 –)7 – 14 mm long; leaf blades ovate, narrowly ovate to elliptical, (2.5 –)3.5 – 7(– 9) mm long, (1 –)1.5 – 3(– 5) mm wide, acute at tip, subrounded to broadly cuneate at base, glabrous above, closely villous to glabrate beneath; petioles broadly winged, 0.5 – 1 mm wide, partially achlorphyllous, shorter than (in small leaves) to longer than leaf blades, often curved. Flowers congested in alternate axils in glomerate 2 – 8-

flowered spikes; bracts ovate, 1.3 – 1.5 mm long, 1.2 – 1.4 mm wide, cupped, rounded at tip, thick cream-white membranous, glabrous; paired bractlets broadly ovate, 1.7 – 2.1 mm long, 1.2 – 1.4 mm wide, textured as bracts; calyces 3.2 – 4 mm long; calyx tubes borne on a slender, densely villous, cylindrical pedicel 0.8 – 1 mm long, 0.3 mm in diameter; calyx tubes campanulate, 1.5 – 1.8 mm long, densely villous with crinkled hairs to 1.3 mm long, 5-veined, without perianth fibrous system; sepals notably unequal, oblong-ovate, 1.2 – 1.5 mm long, 3 broadest lobes 0.7 – 1.1 mm wide, 2 narrower lobes 0.5 – 0.7 mm wide, obtuse to rounded, strongly cupped with margin often incurved even over tip in broad lobes, buff-white, thick, opaque-membranous, reflexed at anthesis, eventually erect, midvein extending into lower half or only half way to tip, weakly villous near base outside, otherwise glabrous; stamens borne at top of calyx tube, basal filament tubes 0.1 – 0.15 mm long; free filaments 0.1 – 0.15 mm long; anthers light yellow, oblong, 0.23 – 0.26 mm long, exserted at throat; mature ovaries 1.7 – 2.0 mm long, 1 – 1.2 mm wide; styles 0.2 mm long, stigmatic lobes 0.1 mm long. Fruits utriculate, ovary wall slight brownish below style; seeds compressed ovoid, 1.1 mm long, 0.8 mm wide, 0.6 – 0.7 mm thick, shiny, reddish brown.

Guilleminea elongata is known to me only from the type collection. Vegetatively it is similar to *G. densa* but differs from *G. densa* by: 1) its persistent rosette of leaves; 2) its thicker membranous, opaque, ivory-white bracts-bracteoles; 3) its thicker, more opaque, yellowish-white, glabrous sepals with entire, distinctly incurved margins; 4) its distinct pedicel, ca. 1 mm long, that separates the bract-bracteoles from the calyx tube; 5) its overall longer flower length; 6) the unequal-sized sepal lobes with those opposite the ovary margins being narrower and slightly shorter; 7) the lack of any fibrous thickening system in the calyx tubes.

Mears noted that the stamen tube of *G. elongata* is completely adnate to the calyx tube, and that flowers are to 5 mm long, but as in *G. densa* a distinct filament tube 0.1 – 0.15 mm long is borne at the calyx tube throat and no flowers were observed over 4 mm in total length. The longer overall flower length is caused primarily by the elongated pedicel (ca. 1 mm long). In contrast, pedicels, when present, are only 0.2 – 0.3 mm long in *G. densa*. Observations on the microstructure of bracts and calyx lobes reveal that cell size in both is the same as in *G. densa*, but the cell walls are measurably thicker in *G. elongata*, with the paired tangential walls being 1.5 *vs.* 2.0 um thick in bracts and 5.6 *vs.* 8.3 um thick in sepals for *G. densa* and *G. elongata* respectively.

Whether this indeed represents a distinct species or is only an aberrant individual can only be determined when more material is made available.

It is certainly disjunct and distinct phenetically and it is deemed best to recognize it as a separate species at this time.

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DEVELOPMENTAL CONTROL IN ANIMALS AND PLANTS. 1984. C. F. Graham and P. F. Wareing. Second edition. Blackwell Scientific Publications. 519 pp. Paper, $37.00.

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CALYCANTHUS BROCKIANA (CALYCANTHACEAE), A NEW SPICEBUSH FROM NORTH CENTRAL GEORGIA

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ABSTRACT

Calycanthus brockiana occurs within populations of *Calycanthus floridus* var. *floridus* and var. *glaucus* and is characterized by pale yellowish-green flowers and lighter textured leaves. It breeds true under selfing but fails to produce seed when crossed with *C. floridus* var. *floridus*.

Calycanthus was recently monographed by Nicely (1965), with subsequent nomenclatural modifications made by Boufford and Spongberg (1981) and Hardin (1984). Nicely (1965) and Boufford and Spongberg (1981) recognize two varieties of one species in the southeastern United States: *Calycanthus floridus* L. var. *floridus* and *C. f.* var. *glaucus* (Willd.) Torrey & Gray. Observations on spicebushes growing along the southeastern slopes of the Smoky Mountains in Lumpkin, White and Habersham counties, in north central Georgia reveal the presence of distinctive pale yellowish-green-flowered plants interspersed among both *Calycanthus floridus* var. *floridus* and *C. f.* var. *oblongifolius*. These plants were initially considered to represent the equivalent of an albino-flowered form of *C. floridus* var. *floridus* with which they agree in leaf vestiture. However, they differ also from sympatric populations of *Calycanthus floridus* in their lighter-colored (not reddish) leaf veins (undoubtedly a pliesomorphic albinistic characteristic), by the similarity in secondary and tertiary-quaternary venation, (in var. *floridus* secondary venation is thicker than tertiary-quaternary venation), in their more cuneate to narrowly rounded (not broadly rounded) leaf bases, their thinner, more pliable or softer leaf texture, their solitary (not paired) flowers at nodes, and their smaller, more pubescent seeds ca 6 mm long (not 10 mm long) with short, curved (not longer, straighter) hairs. This combination of characteristics strongly serves to distinguish this taxon from the more common, sympatric plants of *Calycanthus floridus* var. *floridus*.

Agamospermy has been reported in plants of *Calycanthus floridus* var. *floridus* by Schuroff (1923) and pollination is necessary for development of endosperm, without which the embryo does not grow (Wood 1958). If

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these light-flowered individuals are agamospermous, this could explain their presence in moderate numbers and their lack of intergradation with sympatric individuals of typical *C. floridus*. Casual investigations of breeding relationships in transplanted, garden-grown plants, reveal that plants of the new taxon set no seed when bagged to exclude insect visits. But viable, germinatable seeds were produced when the new taxon was self crossed. No seeds were produced in crosses between the new taxon and plants of *C. floridus* var. *floridus*. This would imply that the new taxon could cross among itself but was reproductively isolated from *C. floridus*. These data favor recognition of the new taxon as a distinct species.

CALYCANTHUS **brockiana** Ferry & Ferry f., sp. nov.

Calycanthus floridus proxima a qua imprimis differt cum foliis texturi et venatione tenue sine pigmento rubro et sine pubescente rubro inferior. Glabrate superior, cum foliis formis ellipticus, distalis acuminatus, basilaris angustatus (*C. floridus* basilaris rotundatus-truncatus). Floribus albidus-chloroviridulus peripallidus.

Erect, branched shrubs 1 – 2(– 3) m tall, initially slender, with age forming lateral proximate shoots and becoming more rounded; young branches yellow-green with age reddish brown, hirtellous and strigose with short, erect to antrorsely curved hairs (0.02 –)0.1 – 0.3 mm long. Leaves ovate, oblong-ovate, elliptical to oblong-elliptical, (4.5 –) 5 – 11.5 cm long, (17 –)23 – 52 mm wide, acuminate below a rounded to acute tip, broadly cuneate to somewhat rounded, often oblique at base, entire, thin, softly flexible, pale lime-green, scabrous with widely scattered pustulate-based, curved, deciduous hairs 0.1 – 0.2(– 0.3) mm long, with age becoming smooth and glabrate above, glaucous, openly, persistently villous-pilose with erect to curved hairs 0.2 – 0.7(– 1.1) mm long beneath, mid and secondary veins pale green, raised beneath, midveins more strongly vestitured than lamina on both surfaces; petioles 4 – 9 mm long, vestitured as young stems. Flowers terminating new leafy shoots of season with usually only one shoot (flower) produced at a paired node; pedicels 11 – 13 mm long, vestitured as young stems; flowers 3.6 – 4 cm in diameter (pressed); tepals 25 – 26, pale yellowish-green; outermost tepals linear, linear-elliptical, 12 – 15 mm long, 2.5 – 3.5 mm wide; middle tepals more oblong-oblanceolate to narrowly obovate, 12 – 16 mm long, (2.5 –)4 – 5 mm wide; inner tepals oblong oblanceolate, spatulate to narrowly elliptical, 7.5 – 10 mm long, (1.5 –)2.5 – 3.5 mm wide, all acute, sometimes obliquely acute at tip, slightly tapering to a broad base, thickish, entire, strigose with antrorse hairs 0.1 – 0.2(0.3) mm long on both faces, innermost tepals with white food bodies 0.2 – 0.3 mm long; receptacle subglobose, ca 6 mm long and wide; stamens 12,

filaments 0.5 – 0.6(– 1.1) mm long, 0.5 – 0.6 mm in diameter; anthers (0.8 –)1.7 – 2.2 mm long, terminal connective extension-food bodies clavate, 0.4 – 0.5 mm long, 0.2 mm wide; inner staminodia ca 22, borne on the upper inner receptacle, conicle, 1.5 – 3.5 mm long, to 0.5 – 0.6 mm broad at base, outermost staminodia longer with whitish terminal food bodies ca 0.3 mm long, ca 0.2 mm wide; ovaries ca 24, oblong-ovoid, styles filiform, 2.5 – 3.5 mm long. Seeds pale reddish, ca 6 mm long, closely pubescent with curved hairs.

TYPE: U.S.A. GEORGIA. Lumpkin Co.: 20.6 km SW of Dahlonega, near a dirt road running east-west, E of Juno, 10 May 1982, *R.J. Ferry Sr.* 637 (HOLOTYPE: GA; ISOTYPE: TEX).

The new species is distinguished by the characteristics noted above. The largest population of *Calycanthus brockiana* occurs in Lumpkin County, Georgia, 20.6 km southwest of the county seat of Dahlonega with extremely sparse representations noted in the Lake Russell Wilderness Area south of Mount Airy in Habersham County, and 4.8 km west of Robertstown in White County.

The species is respectfully named in honor of Dr. Dorothy L. Brock of North Georgia College, Dahlonega, Georgia, scientist, mentor, and humanist.

ACKNOWLEDGMENTS

We want to thank Dr. James Henrickson and Dr. B. L. Turner for their help and allowing us to use the herbarium at UT.

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FROM THE PREFACE. "In this fourth edition, BIOLOGY OF PLANTS remains true to its original goals: to present the basic information about plants in a solid, well-illustrated, and interesting way. As in previous editions, we pay special attention to what we think of as the book's interlocking themes: (1) the plant body as the dynamic result of the processes of growth and development mediated by chemical interactions; (2) evolutionary relationships as the guide to understanding form and function in organisms; and (3) ecology as a way of emphasizing our dependence on plants to sustain our lives and those of all other living organisms."

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FROM THE PREFACE. "This book is intended primarily for the amateur field botanist or naturalist. As with the first edition, this one is generally in the style of a field guide, with identification keys revised and updated to accomodate new discoveries and changes in nomenclature, diagrams where I deemed them useful, descriptionsof the plants, distribution information, and ecological notes based primarily on my own field observations and experiences." Anyone interested in orchids should have a copy of this book.

RECENT COLLECTIONS AND A REDESCRIPTION OF *AMSONIA LUDOVICIANA* VAIL (APOCYNACEAE)

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ABSTRACT

Amsonia ludoviciana (Apocynaceae), recently placed under review for possible listing as an endangered species by the United States Department of the Interior, is shown to be of very limited occurrence in north central Louisiana. Populations discovered in 1983 and 1985 represent the only known natural populations of the species and total fewer than 1000 individuals. Because the only complete description of *A. ludoviciana* was published nearly 60 years ago and was based on observations of only three specimens, a redescription of the species is provided.

Amsonia ludoviciana was first described by Vail in Small (1903) from material collected in southern Louisiana during the early part of the nineteenth century. No additional collections of the species were made, however, until the plant was rediscovered by Small near Bay St. Louis, Mississippi, in 1926 (Small 1932). During the ensuing fifty-one years *A. ludoviciana* was collected from nature only 7 times, all of these collections being from the longleaf pine region of central Louisiana (Natchitoches, Rapides and Vernon parishes). Between 1978 and 1983, fieldwork conducted by this author and by several graduate students and faculty members of the Department of Botany, Louisiana State University at Baton Rouge, failed to locate any natural populations of *A. ludoviciana* and it was feared that the species might have become extinct in its natural habitat. These observations eventually led both the U.S. Department of the Interior (1985) and the Louisiana Natural Heritage Program (1986) to place the species under consideration for possible listing as an endangered plant.

In early April, 1983, a single population of *A. ludoviciana*, consisting of approximately 300 individuals, was discovered by this author in northwestern Rapides Parish at the intersection of Louisiana State Highways 8 and 118. The population of several hundred individuals was located on a tract of timber company land that had apparently burned during the preceding year. The site was dominated by slash pine (*Pinus elliotii* Engelm.) and fire-killed individuals of wax myrtle (*Myrica cerifera* L.); very little groundcover was present except for the Amsonias. A few weeks later

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an additional population was discovered in neighboring Grant Parish (see specimens examined, below).

During a follow-up visit to the area in April, 1985, several additional populations of *A. ludoviciana* were discovered. Most of these were along La. 118 in Natchitoches Parish, between Mora and Kisatchee, west of the 1983 locality. A single small population was found in Bienville Parish, west of Castro. In each instance the plants were growing on open, moderately disturbed sites such as highway rights-of-way and the population size was under 100 individuals.

Apparently, *A. ludoviciana* is more common than has previously been believed, although it is nowhere abundant. The species, at present, seems to consist of a number of relatively small populations scattered throughout the longleaf pine region of Louisiana (Fig. 1). Further fieldwork to accumulate additional data on its distribution and habitat preferences would be desirable before any action is taken on its listing as an endangered species.

In light of its sporadic occurrence it is fortunate that *A. ludoviciana* has been cultivated at two botanical preserves: Brookgreen Gardens, at Murrells Inlet, South Carolina, and Briarwood, the Caroline Dorman Nature Preserve, near Saline, Louisiana. Label data from a specimen on deposit at NCU (*Tarbox and Coker s.n.*) indicate that the plants at Brookgreen Gardens are derived from seeds provided by J.K. Small originating from his 1926 Bay St. Louis collection. Approximately 100 individuals are reported to be doing well at the garden (G.L. Tarbox, pers. comm.). An additional 80 – 100 plants are in cultivation at Briarwood, but no information is available regarding their place of origin (R.L. Johnson, pers. comm.).

The most complete taxonomic treatment of *A. ludoviciana* to date is that presented by Woodson (1928). Because Woodson's treatment was based upon only three specimens, a revised and more complete description is presented here.

TAXONOMIC TREATMENT

AMSONIA LUDOVICIANA Vail in Small, Fl. SE. U.S., ed. 1, 935. 1903.

Herbaceous perennials from a thick, woody rootstock; stems erect, 3 – 6.5 dm tall, sparsely pilose with wavy hairs 1.5 – 2 mm long to glabrous, sparingly branched above. Petioles 1 – 4 mm long or the leaves occasionally sub-sessile, pubescent. Leaves alternate, exstipulate, simple. Leaf-blades elliptic-lanceolate to elliptic-ovate, (3.5 –)4.5 – 7.5(– 9) cm long, (1.2 –)1.5 – 2.5 cm wide, acute at the tip, often somewhat oblique

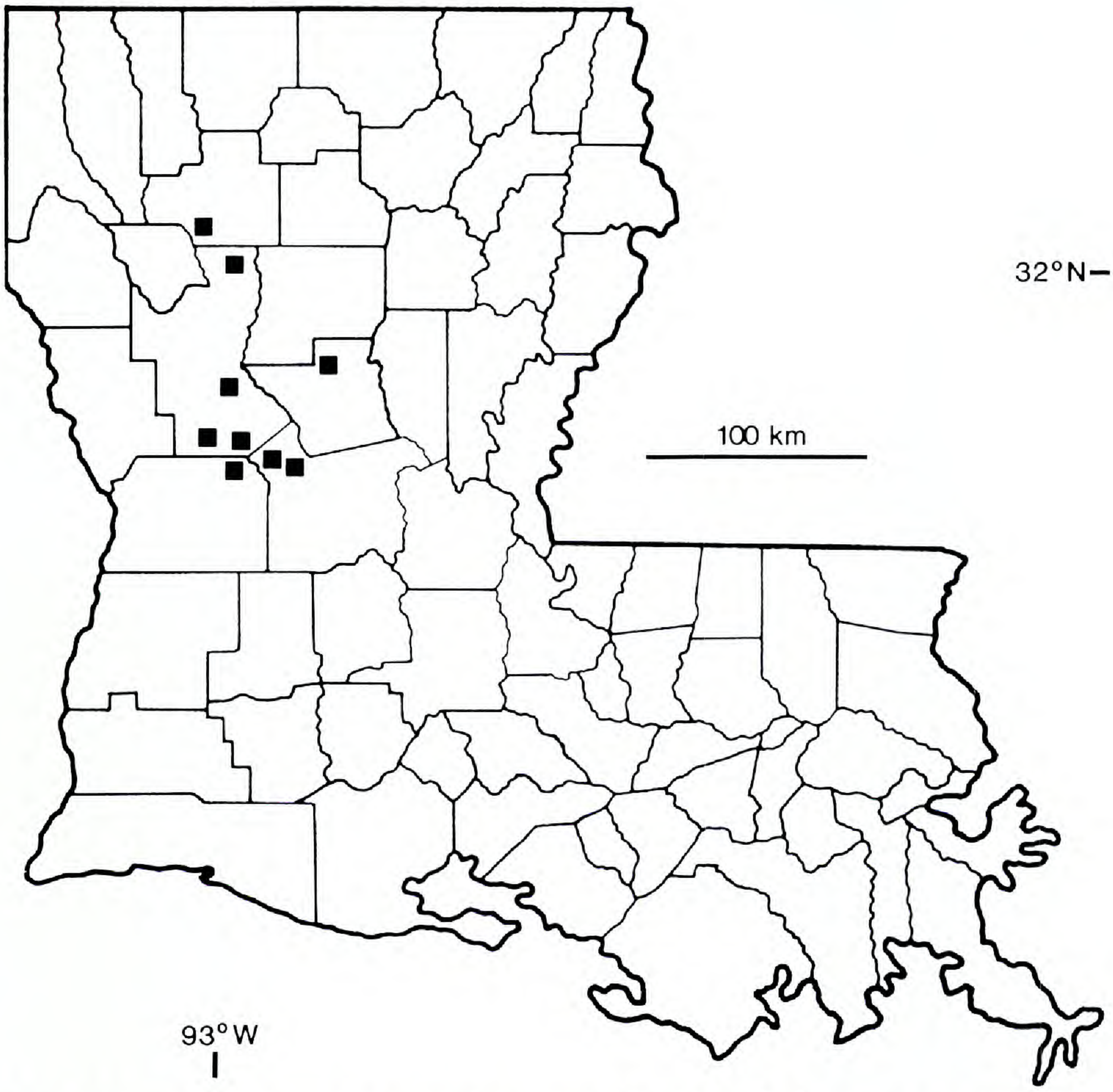

FIG. 1. Known distribution of *Amsonia ludoviciana* in Louisiana. Each square may represent a single collection or several closely-spaced collections.

at the base, at the margins entire, slightly revolute, moderately to densely tomentose below with crooked hairs to 1 mm long, sparsely pubescent to glabrous above. Inflorescence terminal, thyrsiform, bearing 25 − 80 azure flowers. Calyx 5-parted, the lobes triangular to triangular-lanceolate, equal, 0.8 − 1.0(− 1.4) mm long, glabrous. Corolla salverform, pilose externally with shaggy white hairs 1 − 1.5 mm long or occasionally glabrous; tube 6 − 7(− 9) mm long, 1 − 1.2 mm wide at the base, somewhat dilated above the insertion of the stamens, not constricted at the orifice; limb regularly 5-parted, the lobes 5 − 6 mm long, glabrous, spreading. Stigmatic cap about as broad as tall, the stigma truncate. Follicles slender, continuous, 8 − 13(− 16) cm long, densely pubescent with short white hairs 1.2 − 1.4 mm long. Seeds 6 − 10, oblong-ovoid, 6 − 10(− 12) mm long, truncate at both ends, verrucose, dark brown. Chromosome number, $n = 11$.

The relationships of *A. ludoviciana* are with the *A. tabernaemontana* complex of species (Subgenus *Amsonia* Woods.) of the eastern United States. Members of the section are characterized by slender, continuous follicles and a depressed-capitate or truncate stigma (Woodson 1928). The abaxially densely tomentose leaves of *A. ludoviciana* readily distinguish it from all other members of this complex.

Specimens examined: **LOUISIANA. Bienville Parish**: roadside ditch along La. 4, 1 mi W of Castor city limits, 6 Apr 1985, *Lemke 116* (LSU). **Grant Parish**: 2 mi NW of Williana, Kisatchee Natl. Forest, 23 Apr 1983, *Martin 364* (SFRP). **Natchitoches Parish**: sandy roadside, Red Dirt Wildlife Management Area, Kisatchee Natl. Forest, along High Ridge Road, 4 Apr 1977, *Barbour 1270* (LSU); roadside along La 118, 4 mi W of Mora, 7 Apr 1985, *Lemke 118* (LSU); roadside along La 118, 7.0 mi W of intersection with La 8, 7 Apr 1985, *Lemke 119* (LSU); roadside along La 118, 13.3 mi W of intersection with La 8, 7 Apr 1985, *Lemke 120* (LSU); Caroline Dorman Briarwood Nature Preserve on La. 9, N of Campti, 4 Apr 1981, *Pruski and Lemke 2027* (LSU); roadbank at Cypress Branch, 4 mi W of Mora, 30 Apr 1972, *Thomas 28587* (NLU). **Rapides Parish**: along small creek about 2 mi W of Boyce, 22 Mar 1972, *Allen 1836* (LSU); low woods about 3 mi WSW of Boyce, 24 Mar 1972, *Allen 1841* (LSU); Calcasieu River bottoms, E of Vernon-Rapides boundary on Highway 1, W of Flatwoods, 10 Apr 1939, *Brown and Lenz 7688* (LSU); 5 mi S of Flatwoods, 15 May 1970, *Grelen 703* (SFRP); NW corner of intersection of La. 8 and La. 118, 4 Apr 1983, *Lemke 79* (LSU); NW corner of intersection of La. 8 and La. 118, 7 Apr 1985, *Lemke 117* (LSU). **Vernon Parish**: Highway 465 near Simpson, 10 Apr 1966, *Brown 18831* (LSU). **MISSISSIPPI. Hancock Co.**: 10 mi NW of Bay St. Louis, Apr 1926, *Small 56665* (MO, NY). **SOUTH CAROLINA. Georgetown Co.**: Brookgreen Gardens, 20 Apr 1936, *Tarbox s.n.* (NCU); Brookgreen Gardens, 20 Jul 1945, *Tarbox and Coker s.n.* (NCU).

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ANATOMICAL STUDY OF THE *MUHLENBERGIA REPENS* COMPLEX (POACEAE: CHLORIDOIDEAE: ERAGROSTIDEAE)

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ABSTRACT

Leaves of eight species of *Muhlenbergia* composing the *M. repens* complex were analyzed for anatomical detail. Analysis of transverse section and epidermis shows that most species can be clearly defined. *Muhlenbergia plumbea* is the most unique species in the complex; characters by which it differs suggest there is little relationship between it and the other species. Differences between *M. richardsonis* and *M. squarrosa* were not found, supporting the current interpretation that these are conspecific. A few differences between *M. villiflora* and *M. villosa* were found, suggesting that these be maintained as distinct entities. In *M. utilis*, sclerenchyma formed an abaxial girder between the colorless cells and the epidermis as well as between the vascular bundle and the epidermis. Sclerenchyma in *M. fastigiata* was present on the adaxial side or associated with the abaxial side of primary bundles only; secondary bundles were absent and no girders were formed on tertiary bundles. The occurrence of rows of short cells on the epidermis appears to be correlated with the presence of sclerenchyma below the epidermis. The anatomical data suggests there are seven well defined taxa, two of which (*M. villiflora* and *M. villosa*) are distinguishable by only a few characters.

INTRODUCTION

The genus *Muhlenbergia* Schreb. consists of about 125 species with a center of distribution in the southwestern United States and northern México. In general these species are found in hot arid habitats, although some species occur in other habitats such as moist shaded woodlands (subg. *Muhlenbergia*) and alpine meadows [*M. richardsonis* (Trin.) Rydb. and *M. filiformis* (Thurb.) Rydb.].

The present study involves species in the *Muhlenbergia repens* complex. Members of this complex are distributed throughout North America (excluding the southeastern United States) and in the Andean highlands of South America. As defined here, this complex consists of eight species: *M. fastigiata* (Presl) Henrard, *M. plumbea* (Trin.) Hitchc., *M. repens* (Presl)

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Hitchc., *M. richardsonis* (Trin.) Rydb., *M. squarrosa* (Trin.) Rydb., *M. utilis* (Torr.) Hitchc., *M. villiflora* Hitchc., *M. villosa* Swallen. This complex is characterized by a rhizomatous perennial habit with short culms seldom exceeding 20 cm, short involute leaf blades, and short contracted inflorescences with awnless or mucronate spikelets. Most of the species occur in the southwestern United States and adjacent México. *Muhlenbergia plumbea* typically grows larger than other members of this complex and can have an open inflorescence. Charlotte Reeder (per. comm.) suggested the inclusion of *M. plumbea* because it is often confused with *M. richardsonis*. Little is known of the variation among taxa within this complex and there is an apparent overlap in morphological characters and sympatry in distribution.

Anatomical characters of the leaf have been used in the classification of the grass family for over 100 years. For a review of the literature see Brown (1958). The genus *Muhlenbergia* was shown to possess typical chloridoid anatomy (Brown 1958) which has been correlated with the C_4 photosynthetic pathway and specifically the NAD-me subtype (Brown 1977).

Previously, leaves of three species in the *Muhlenbergia repens* complex had been analyzed for anatomical detail. Soderstrom (1967), in his study of subgenus *Podosemum*, analyzed *M. richardsonis* and *M. plumbea* as well as many other species not in subgenus *Podosemum*. He found that the anatomy of *M. richardsonis* and *M. asperifolia* (Nees & Mey.) Parodi was similar to that found in section *Epicampes*, except that the phloem of the primary bundles was not sclerosed. *Muhlenbergia plumbea* was very different and more closely resembled *M. arizonica* Scribn. The anatomy of *M. utilis* was observed by Brown (1977), although he was primarily looking at photosynthetic subtypes rather than anatomical detail in that study.

Other studies have shown that characters of the leaf blade in transverse section and surface view may be important in the classification of grasses at all ranks, including species rank (Lersten and Pohl 1969; Renvoize 1981, 1983; Sanchez 1979, 1983; Stieber 1982; Tateoka et al. 1959; Webster 1983; Yates 1966). For this reason, species of the *M. repens* complex were analyzed to determine if anatomical features could consistently be used to differentiate taxa. Of specific interest was the relationship in the subcomplexes of *M. richardsonis-squarrosa* and *M. villiflora-villosa*, because these entities could not be separated consistently on the basis of gross morphology.

MATERIALS AND METHODS

Specimens were obtained from our own field collections, collections of collaborators, and herbarium specimens. Specimens used in the analysis are

listed in Table 1. Leaf blades were selected from no less than three (usually five) populations from across the geographic range of each species. At least three leaf blades were selected from each plant so that leaf transverse section and adaxial and abaxial epidermis could be analyzed. Leaves were selected from the midculm region, excluding the lowermost leaf and the leaf subtending the inflorescence. Leaf blades were placed in Kodak photo-flo and rehydrated. Leaf blades were then transferred to 70% ethanol, dehydrated, and embedded in paraffin using the standard techniques as described by Berlyn and Miksche (1976). Sections 10 – 15 μm thick were made with a rotary microtome, stained with safranin and fast green, and made permanent with Permount. Leaf blades used for epidermal preparations were placed flat on a microscope slide, the epidermis scraped clear with a razor blade, inverted, stained with Chlorazole Black E, and made permanent with Euparal. Features of the leaf epidermis in the *M. repens* complex reported here are those primarily of the abaxial surface. The epidermis of the adaxial surface was in all but a few cases not obtainable because of the deep furrows between the bundles on the adaxial surface. The anatomical terminology used follows that of Metcalfe (1960) and Ellis (1976, 1979). In addition, there are characters of specific interest in *Muhlenbergia* that were discussed by Soderstrom (1967). Complete descriptions of each species are given in Morden (1985).

LEAF BLADE IN TRANSVERSE SECTION

The lamina of species in the *M. repens* complex is outwardly bowed to U-shaped and moderately to deeply furrowed adaxially between the veins (Fig. 1, 3 – 7, 9, 11 – 15). The notable exception to this is *M. plumbea*. Here the blades are folded (keeled) with a pronounced midrib (Fig. 2); and the furrows between the veins are very shallow (Fig. 10), except adjacent to the midrib (Fig. 8).

Three distinct types of vascular bundles could be identified in leaves of this complex: primary, secondary and tertiary (Soderstrom 1967) corresponding to the first, second, and third order vascular bundles of Ellis (1976). In all cases secondary and tertiary bundles were the same size in this complex. For purposes of reference, secondary bundles were identified as vascular bundles with the associated chlorenchyma interrupted adaxially or abaxially by a sclerenchyma girder, and tertiary bundles with continuous chlorenchyma around the vascular bundle. Often this was correlated with the interruption of the bundle sheath by sclerenchyma in secondary bundles, and intact bundle sheaths in tertiary bundles.

Soderstrom (1967) distinguished primary bundles from secondary and tertiary bundles on the presence or absence of metaxylem in the vascular

TABLE 1. Specimens used in analysis of leaf transverse sections and epidermal scrapes. Unless otherwise indicated, specimens used in the analysis are deposited at TAES. Where duplicate specimens are listed, an asterisk (*) indicates the specific specimen used in the analysis.

MUHLENBERGIA FASTIGIATA. ARGENTINA. **Jujuy**. Yavi: Pumajuasi *Meyer 14897* (*GH, NY). BOLIVIA. **Potosi**. Bustillos: Uncia, Karachi, *Renvoize & Cope 3810* (MO). PERU. **Junin**. Yauli: Pachachaca. *Asplund 11624* (NY). **Tacna**. Tacna: Cord. Volcan Tacora, Ancara, *Werderman 1138* (NY, *US).

MUHLENBERGIA PLUMBEA. GUATEMALA. *Koninck 31* (US). MEXICO. **Distrito Federal**. Valley of México, *Pringle 6617* (CAS, GH, *MO, MSC, NY, US). **Puebla**. San Marcos, *Hitchcock 6525* (US).

MUHLENBERGIA REPENS. MEXICO. **Baja California**. La Laguna, *Leon 217*. **Coahuila**. Botany garden at UAA"AN", **Buenavista, Saltillo,** *Morden & Hatch 505*. UNITED STATES. **Arizona**. Apache Co.: 12 mi S of Springerville on Hwy 666, *Morden 668*. **Colorado**. Las Animas Co.: Raton Mts., New Mexico State line, *Griffiths 5449* (GH, *US). **New Mexico**. Catron Co.: San Miguel Co.: 1 mi S of Las Vegas, *Morden 571*. **Texas**. Jeff Davis Co.: 17 mi S of Kent in canyon on Hwy 118, *Morden 684*. **Utah**. Kane Co.: Mt. Carmel, small patch within sagebrush on hillside above E Fork of Virgin River, *Morden 649*.

MUHLENBERGIA RICHARDSONIS. UNITED STATES. **California**. El Dorado Co.: South Lake Tahoe near Trout Creek, *Morden 623*. **Colorado**. Larimer Co.: 2 mi E of jct on 34 near Estes Park, *Morden 595*. **Nevada**. Elko Co.: 8 mi S of Wells toward Angel Lake, *Morden 617*. **New Mexico**. Taos Co., 1 mi SE of Tres Piedras, *Morden 578*. **Utah**. Rich Co.: 8.5 mi S of Garden City on Hwy 30, *Morden 601*. Wasatch Co.: 7 mi W of Hanna on Hwy 35, *Morden & Johansen 606*.

MUHLENBERGIA SQUARROSA. MEXICO. **Baja California**. Tasajera trail N of Ranch Viejo, *Moran 24496*. UNITED STATES. **California**. Tuolumne Co.: Yosemite National Park, upper end of Tuolumne Meadow, *Morden 630*. **Utah**. Rich Co.: 8.5 mi S of Garden City on Hwy 30, *Morden 602*.

MUHLENBERGIA UTILIS. MEXICO. **Chihuahua**. 50 mi N of Chihuahua, *Gould 8911* (MO, *TAES). **Coahuila**. Chorro No. 5, 25 km S of Saltillo, Hwy 57, *Morden, Hatch, & Valdés R. 525*. **México**. 55 km NW of Toluca on Mex 15, *Brunken & Perino 425* (MO, *TAES). UNITED STATES. **Texas**. Kendall Co.: Hillingdon Ranch, 4 mi W of Old San Antonio Road, *Morden 546*.

MUHLENBERGIA VILLIFLORA. MEXICO. **Coahuila**. Rancho Experimental "Los Angeles," ca 45 km S de Saltillo, *Valdés R. y Vasquez s.n.* Hidalgo. 5 mi W of Pachuca, *Reeder & Reeder 4294* (US). **Nuevo Leon**. 12 km E of Hwy 57 on Hwy 58, *Morden, Hatch, & Valdés R. 519*. **San Luis Potosi**. 15 mi NW of Matehuala, *Reeder & Reeder 4508* (US). **Zacatecas**. UAA"AN" experimental ranch, 3 km E of Mex Hwy 45, 32 km S of jct with 54 to del Oro, *Morden, Hatch, Valdés R., 510*.

MUHLENBERGIA VILLOSA. UNITED STATES. **New Mexico**. Otero Co.: E of Orogrande on Otero Mesa, *Spellenberg 4565* (LL, *NMC, NY). **Texas**. Glasscock Co.: 15 mi S of Stanton on Hwy 137, *Morden 559*. Hudspeth Co.: 25 mi W of Cornudas on Hwy 180, *Morden 682*; 10 mi N of Allamore, *Reeder & Reeder 5168* (RM).

bundle, respectively. Primary bundles have a well-developed mestome sheath interrupted on the abaxial (and often adaxial) side by sclerenchyma (Fig. 8 – 15). The sclerenchyma is continuous with the mestome sheath and forms a girder between the abaxial epidermis and the bundle. In most cases an I-beam construction (Gould 1968) across the entire thickness of the leaf is formed. Secondary and tertiary bundles are identical in all characters except those mentioned previously. The mestome sheath is often discontinuous in these bundles and in many cases difficult to distinguish from the protoxylem elements. Secondary bundles are interspersed

between the primary bundles while tertiary bundles are generally restricted to the leaf margins. Notable exceptions to this are *M. fastigiata*, in which secondary bundles are absent, and *M. plumbea*, which has tertiary bundles sporadic throughout the leaf as well as at the margins.

Two types of parenchyma bundle sheath cells are present in the complex. The most common condition is sheath cells with straight radial walls and inflated (rounded) tangential walls. In two species, *M. fastigiata* and *M. villiflora* (Fig. 9 and 14), bundle sheaths differ by having the outer tangential walls straight, angular, or slightly inflated.

The distribution of sclerenchyma in the leaf is an important taxonomic character. The positioning of the strand relative to the vascular bundle is consistent within each species. In most cases, sclerenchyma is present abaxial and adaxial to the costal zone (at least adjacent to the epidermis). *Muhlenbergia fastigiata*, however, does not have sclerenchyma abaxial to the tertiary bundles. In contrast, *M. utilis* has sclerenchyma abaxial to the bundle and in the furrow between the bundles abaxial to the colorless cells.

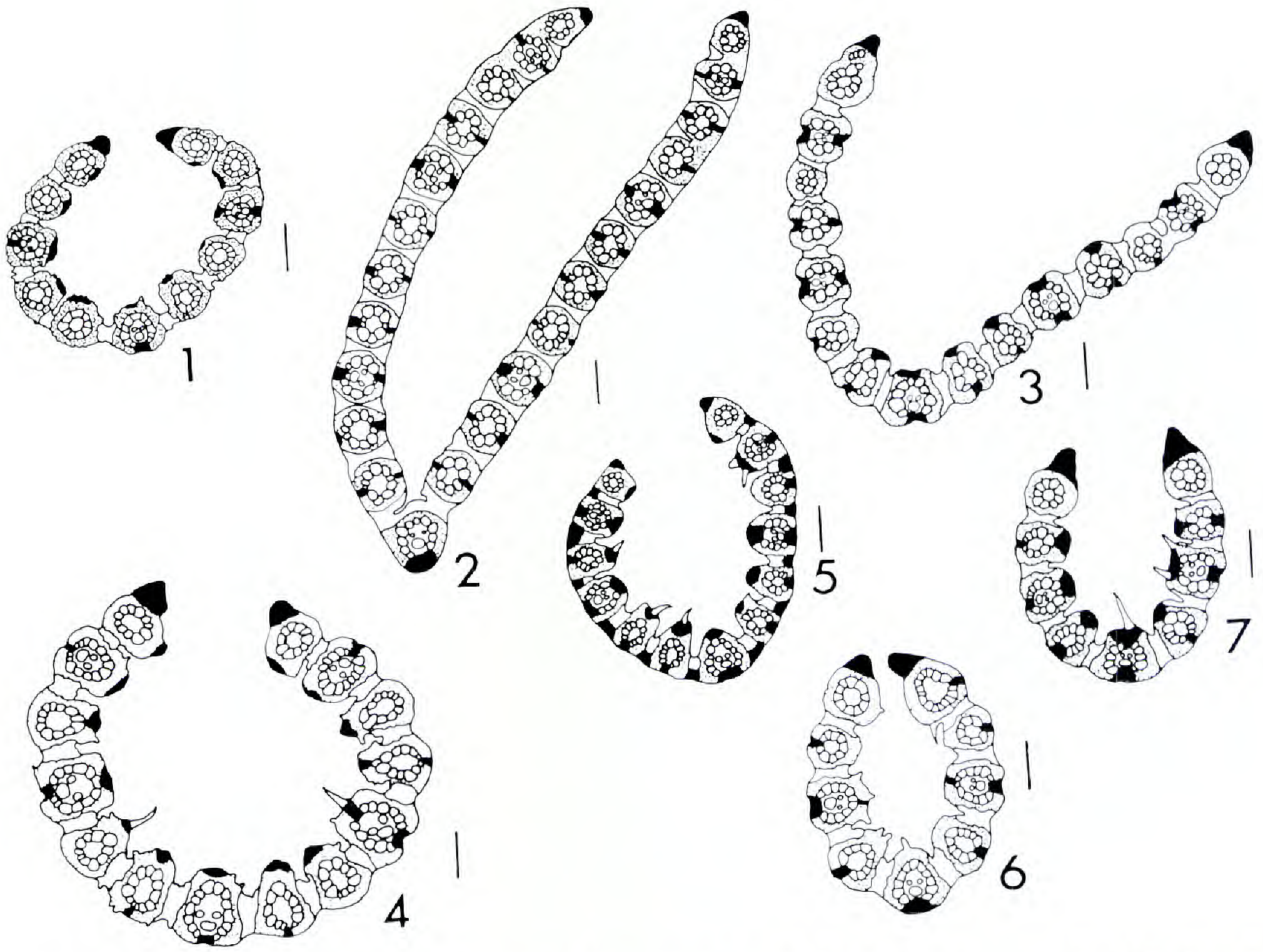
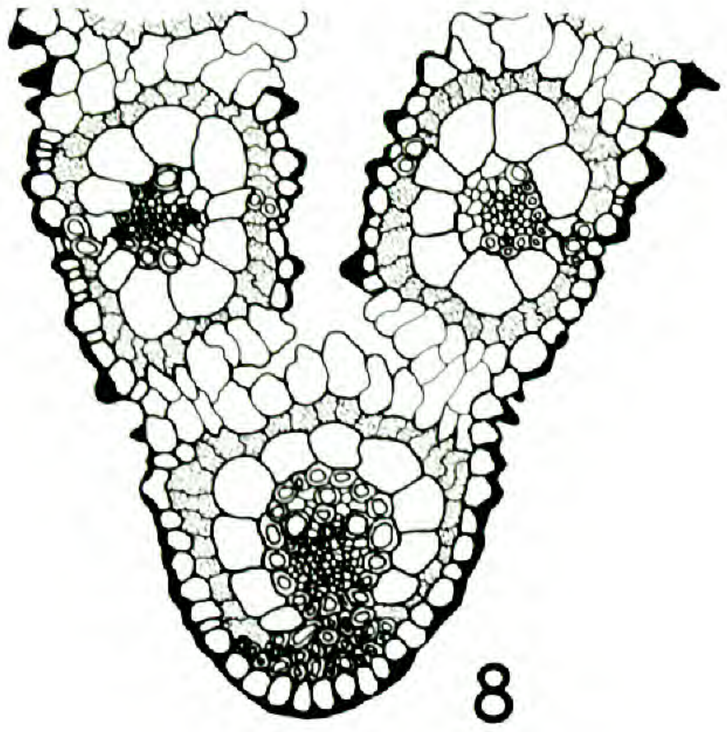
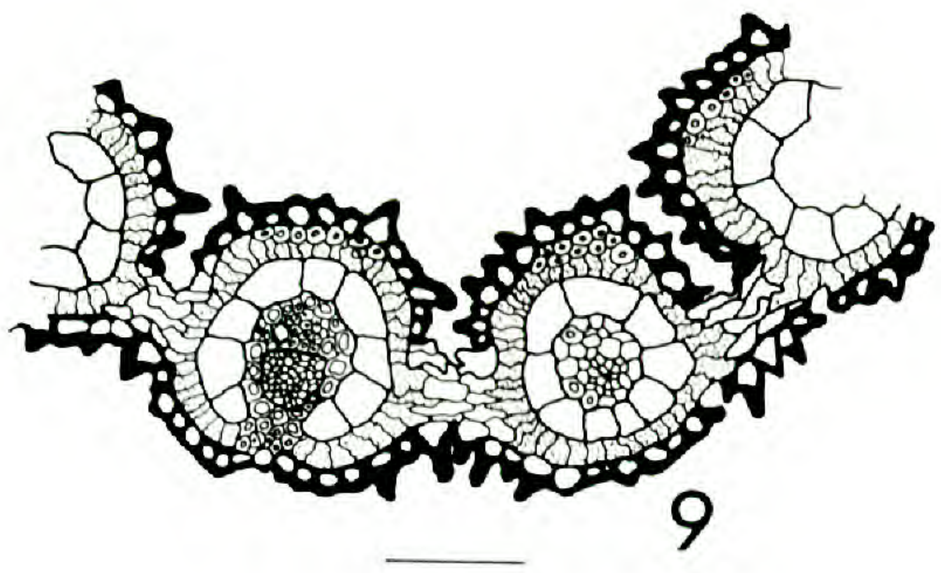
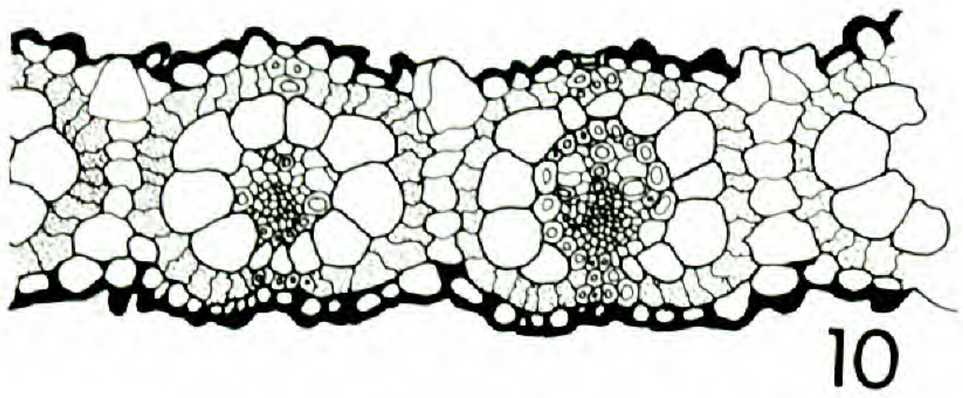


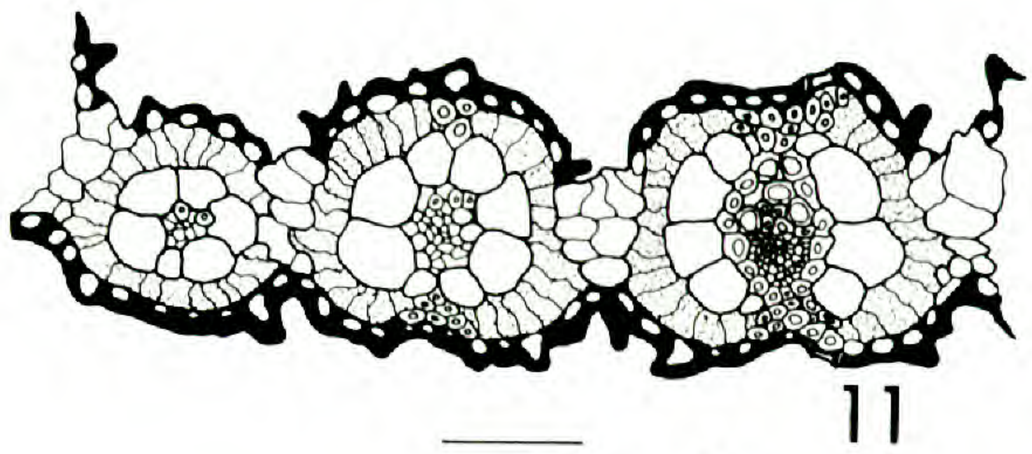
FIG. 1–7. Whole leaf transverse sections of species in the *Muhlenbergia repens* complex. Blackened areas indicate the presence of sclerenchyma. Scale = 0.1 mm. 1. *M. fastigiata*, *Renvoize & Cope 3810*. 2. *M. plumbea*, *Koninck 31*. 3. *M. repens*, *Morden 668*. 4. *M. richardsonis*, *Moran 24496*. 5. *M. utilis*, *Morden 546*. 6. *M. villiflora*, *Valdés & Vasquez s.n.* 7. *M. villosa*, *Reeder & Reeder 5168*.

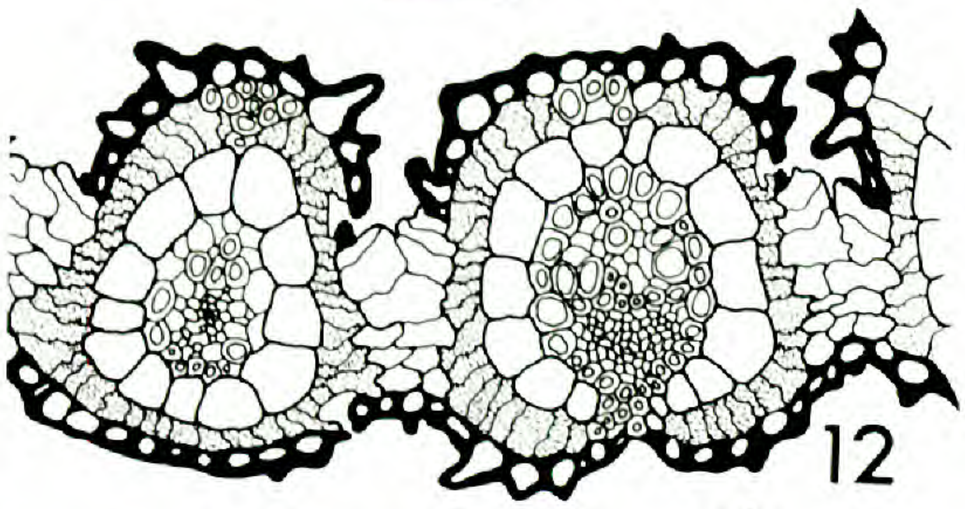
When the sclerenchyma forms a girder between the bundle and epidermis, the radiating chlorenchyma is interrupted. However, when the sclerenchyma forms a cap above or below the bundle, the chlorenchyma may still be continuous around the bundle.

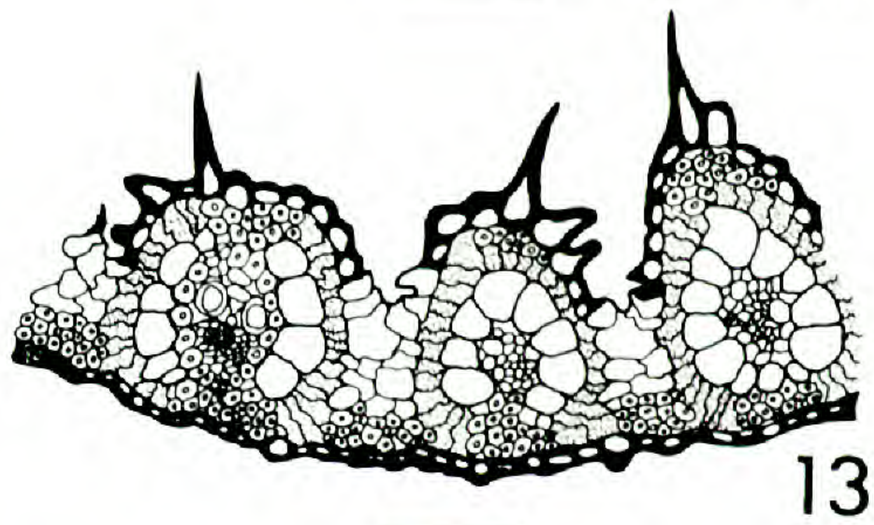


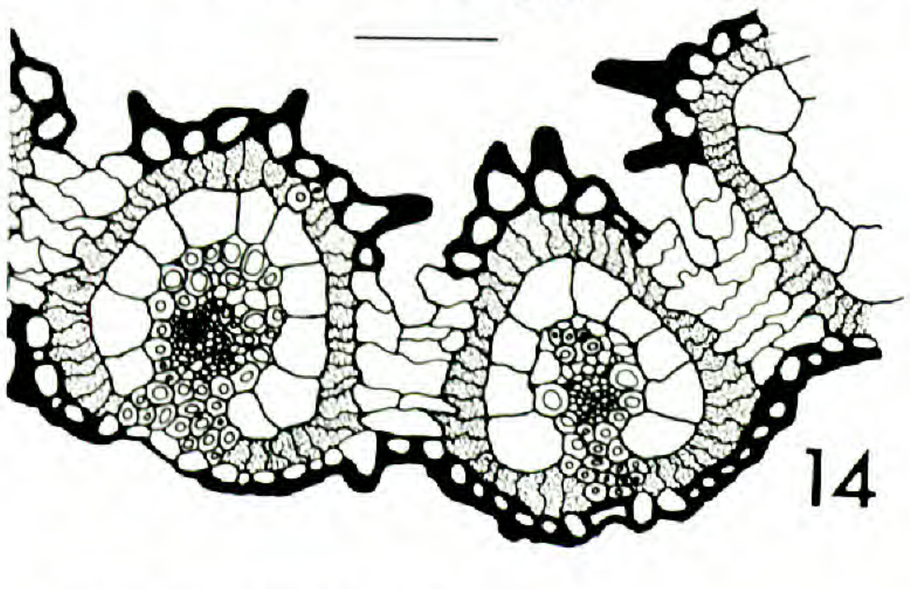












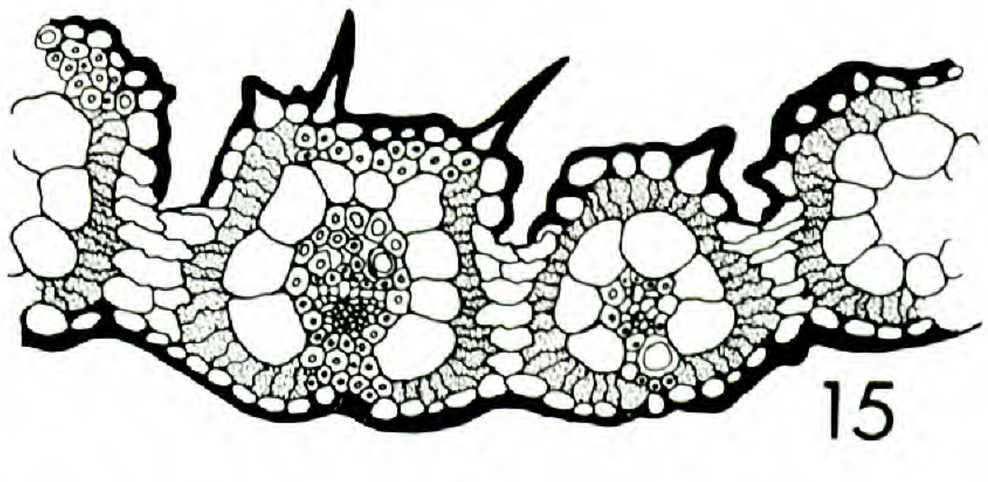


FIG. 8 – 15. Detail of leaf transverse sections of species in the *Muhlenbergia repens* complex. Scale = 0.05 mm. 8. *M plumbea*, midvein and adjacent bundles. 9. *M. fastigiata*, primary and tertiary bundles. 10. *M. plumbea*, primary and secondary bundles. 11. *M. repens*, primary, secondary, and tertiary bundles. 12. *M. richardsonis*, primary and secondary bundles. 13. *M. utilis*, primary and secondary bundles. 14. *M. villiflora*, primary and secondary bundles. 15. *M. villosa*, primary and secondary bundles.

Bulliform cells are of two types in this complex. The most prevalent are specialized, fan-shaped cells found in the furrows of the adaxial epidermis indicating that these leaves have the ability to become flattened or inrolled (*M. repens, M. utilis, M. richardsonis,* and *M. plumbea*). *Muhlenbergia plumbea* has a predominance of bulliform cells adaxial to the midvein and in the adjacent furrows that allows these leaves to fold upon desiccation. In the remaining species (*M. fastigiata, M. villiflora,* and *M. villosa*) relatively unspecialized bulliform cells are present. These leaves are inrolled and may have lost the capacity to become flattened. Colorless cells form a girder-like extension from the bulliform cells to the adaxial epidermis (or sclerenchyma in *M. utilis*). This girder is generally two cells wide (usually one in *M. plumbea*), although there may be some variation.

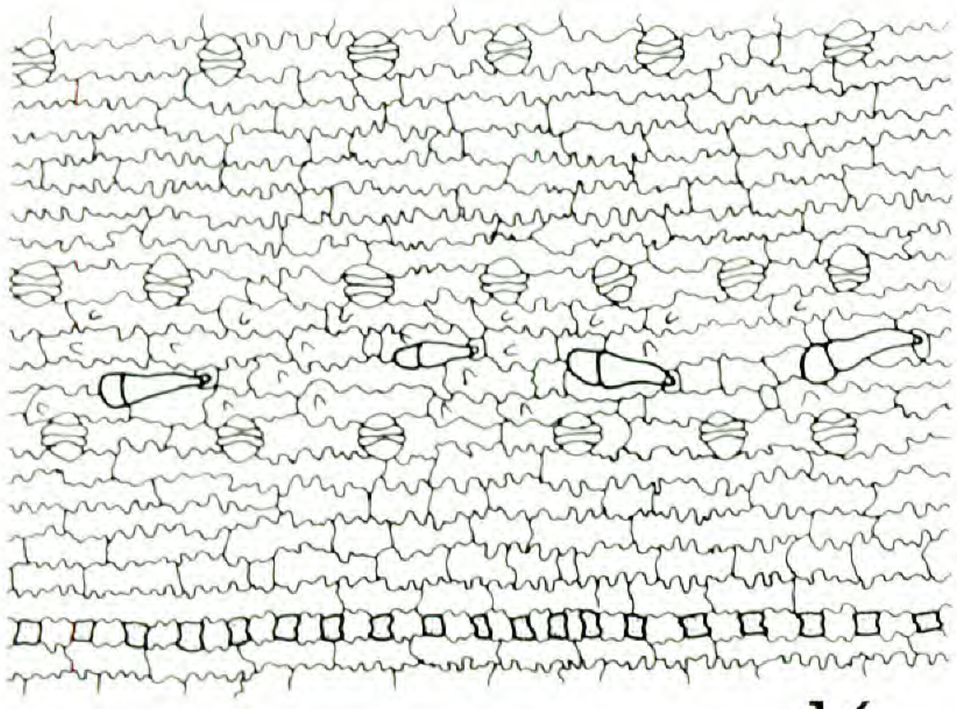
Macrohairs are usually common on the costal zone of the adaxial epidermis and absent from the abaxial epidermis. However, in *M. fastigiata* and *M. plumbea* macrohairs were completely absent from both surfaces. Blades of *M. fastigiata* are densely covered with large papillae on the adaxial surface. Other species are moderately covered with papillae on both leaf surfaces (more densely in the furrows abaxially and on the costal zone adaxially).

LEAF IN SURFACE VIEW

Features of the abaxial and adaxial epidermis are similar for most characters (Fig. 16 – 26). Each surface has two bands of stomata present in the intercostal zone. There is one row of stomata present in each band, occasionally a second row interspersed along the band. In *M. utilis*, this condition is present although deceiving because of the presence of a row of short-cells (cork and silica) in the furrows of the abaxial surface (Fig. 20). Subsidiary cells are usually triangular to low dome-shaped, often both types appearing on a single leaf.

Long-cells are generally long and narrow with strongly sinuous, non-interlocking walls. In *M. villiflora* and *M. villosa* the cells tend to be a little shorter than in the other species, and the walls are more angular (Fig. 21 and 22). Papillae are usually present on both leaf surfaces located distally in the long-cells. Size of the papillae may be variable for each species. Papillae are longer and more abundant in the furrows between costal zones (except in *M. utilis*) and shorter or absent on the costal zones of the abaxial surface. On the adaxial surface papillae are sparse in the furrows (none found on bulliform cells) and more abundant on the costal zone. In *M. fastigiata*, well-developed papillae are present on almost every long-cell of the adaxial surface.

Short-cells are common in the intercostal zone of the abaxial surface in-



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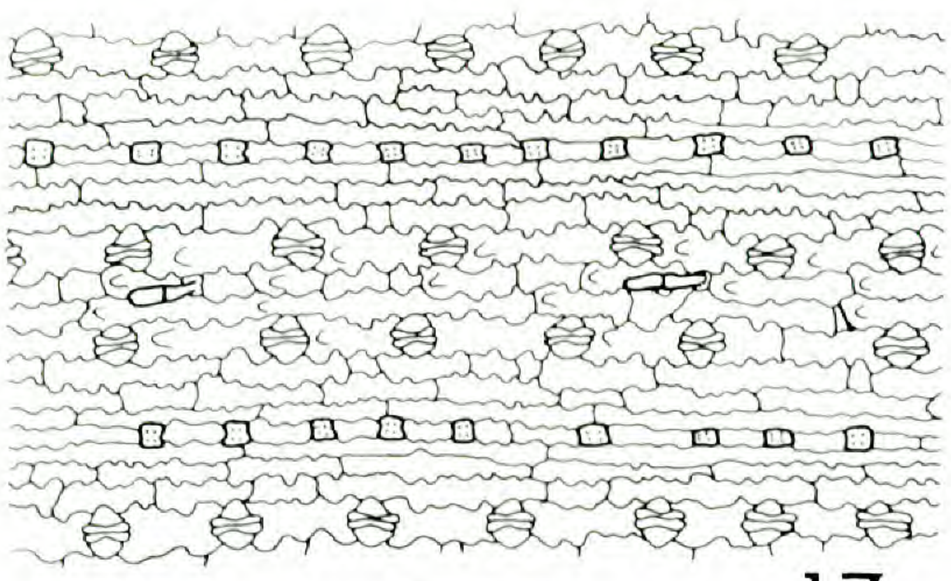

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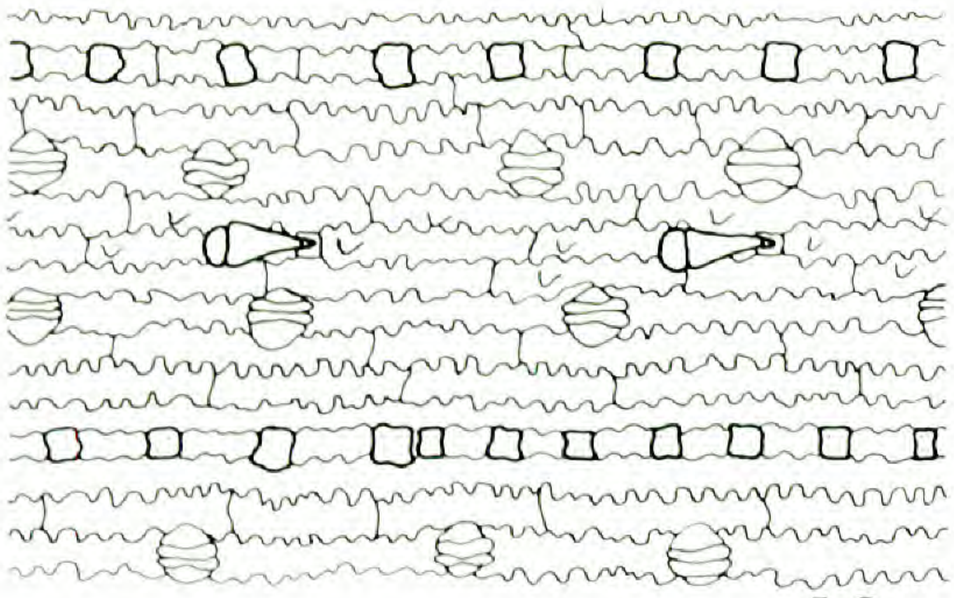

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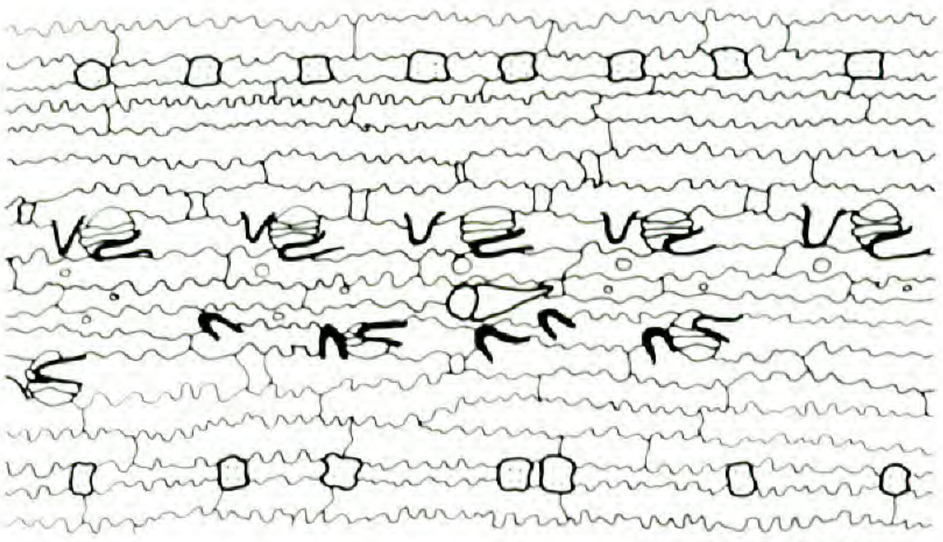

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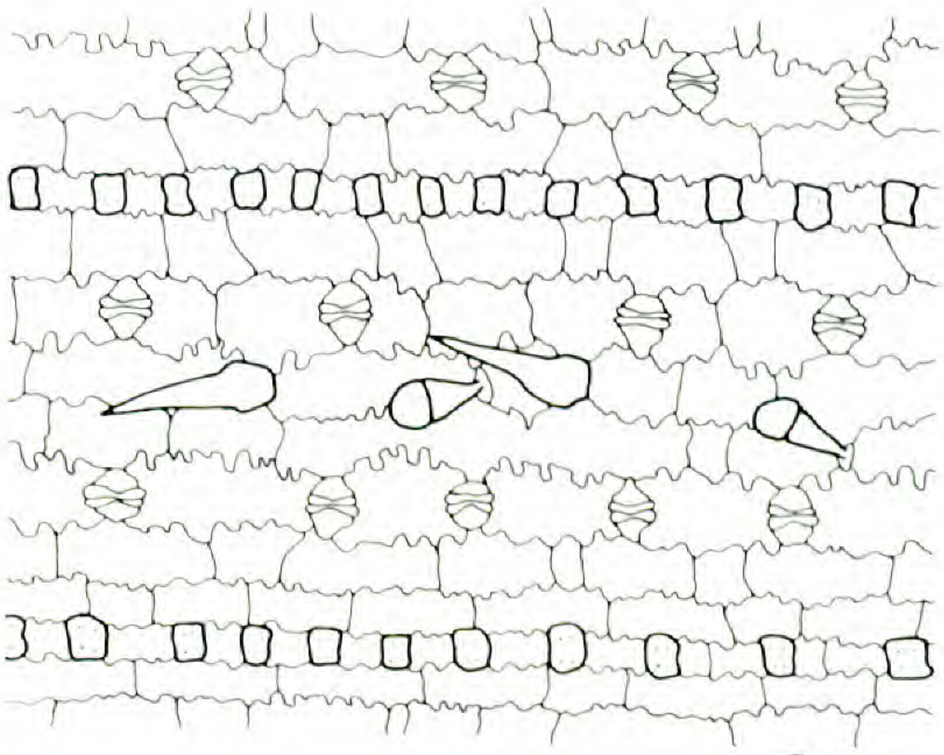

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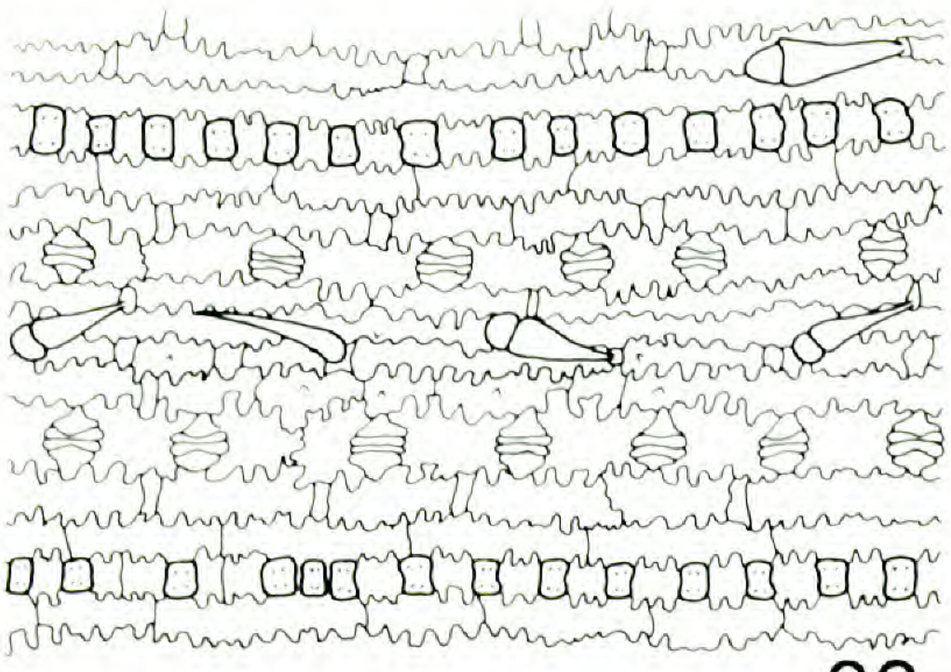

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FIG. 16 – 22. Detail of abaxial surface of leaf epidermis in the *Muhlenbergia repens* complex. Scale = 0.05 mm. 16. M. *fastigiata*, *Asplund 11624*. 17. M. *plumbea*, *Pringle 6617*. 18. M. *repens*, *Morden 576*. 19. M. *richardsonis*, *Morden 623*. 20. M. *utilis*, *Morden 525*. 21. M. *villiflora*, *Morden et al. 519*. 22. M. *villosa*, *Reeder & Reeder 5168*.

terspersed with the long-cells. These cells may also become papillate in *M. richardsonis*. *Muhlenbergia repens* occasionally has a row of two to three short-cells adjacent to each other in furrows of the abaxial surface. Short-cells over the costal zone are arranged in 1 – 3 rows, often more over the midvein, the rows either a continuous string of short-cells, or alternating with long-cells (usually the latter adaxially). Short-cells are of two types: silica-cells with deposits of silica (termed silica-bodies) in the lumen, and cork-cells. Silica-bodies are variably saddle-shaped, in some species also cuboid and cross-shaped. Cork-cells are of various lengths and the lateral walls are sinuous, giving them a dumbbell-shaped appearance when short, otherwise very similar to the long-cells of the intercostal zone except narrower and shorter. Short-cells are absent from the costal region of the smaller (tertiary) vascular bundles in *M. fastigiata*. Costal regions are identified by the position of papillae and bicellular microhairs (in furrows) and the presence of long-cells continuous in the region where short-cells might be expected.

Macrohairs other than prickle-hairs are present in all species except *M. fastigiata* and *M. plumbea*. These hairs are restricted to the costal zone of the adaxial epidermis, except in *M. villiflora* and *M. villosa* where there is also a single row of macrohairs in the furrows of the abaxial epidermis alternating with bicellular microhairs. Prickle-hairs are found along the leaf margins of all species in this complex. In some species prickle-hairs are found on the costal zone of the adaxial surface (fig. 23 and 24), which are often difficult to distinguish from macrohairs.

Bicellular microhairs are clavate, typical of the *Chloris* type described by Metcalfe (1960), except in *M. plumbea* where the hairs are of the *Eragrostis* type (i.e., elongated) (Fig. 17). The size of the hair, although extremely variable in some species (i.e., *M. richardsonis*, *M. villiflora*, and *M. villosa*), seems to be of a consistent length in others (*M. fastigiata*, *M. repens*, and *M. utilis*) and may be useful taxonomically. The variability in length is attributable primarily to the proximal cell; the distal cell shows very little variation throughout the complex. Microhairs are attached to short-cells and may be either randomly distributed in the intercostal zone (*M. plumbea*) or in a single row of the furrow (alternating with macrohairs in *M. villiflora* and *M. villosa*, Fig. 21 and 22). On the adaxial surface, bicellular microhairs are sporadic and associated with the costal region.

RELATION OF SCLERENCHYMA AND SHORT-CELLS

In this study, a relationship between the presence or absence of silica-cells and short-cells on the epidermis and the occurrence of sclerenchyma internally became evident. Based on observation of the abaxial epidermis,

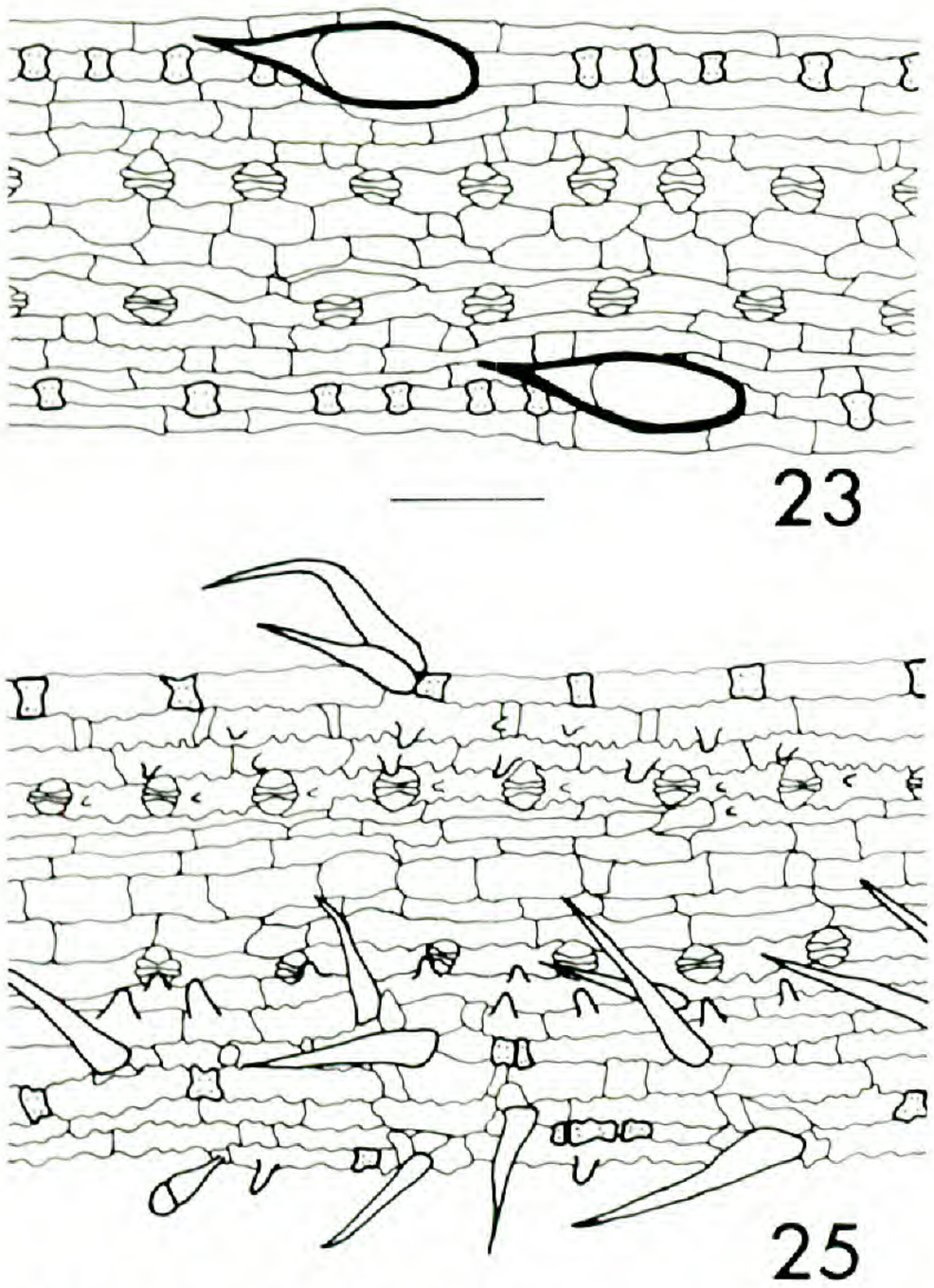

FIG. 23 – 26. Detail of adaxial surface of leaf epidermis in several species of the *Muhlenbergia repens* complex. Scale = 0.05 mm. 23. *M. plumbea*, *Hitchcock* 6515. 24. *M. repens*, *Morden* 505. 25. *M. unilis*, *Morden* 525. 26. *M. richardsonis*, *Morden* 617.

and what can be seen of the adaxial epidermis in cross section, a row of short-cells with silica-bodies is present only if adjacent to sclerenchyma in the subepidermal layer. This is supported by the distribution of sclerenchyma and short-cells in *M. fastigiata* and *M. utilis*. As mentioned previously, *M. fastigiata* does not possess secondary bundles and there is no sclerenchyma abaxial to the vascular bundle. This is correlated with the absence of rows of short-cells over the majority of the costal zones. This condition can be contrasted with *M. utilis*, where in addition to abaxial sclerenchyma girders, strands of sclerenchyma are present immediately below the epidermis of the furrows on the abaxial leaf surface. This is correlated with the presence of a row of short-cells indistinguishable from those over the costal zone.

The number of fibers present in a strand necessary for this association to arise is apparently very small. In many furrows of *M. utilis* only one or two fibers were evident. It appears that with increasing width of the sclerenchyma strand more rows of short-cells are present. This would explain the increase in the number of rows of short-cells over the leaf midvein and on the leaf margin over the sclerenchyma cap in all species.

TABLE 2. Diagnostic characters of leaf anatomy in the *Muhlenbergia repens* complex.

CHARACTER	SPECIES			
	FASTIGIATA	PLUMBEA	REPENS	RICHARDSONIS
TRANSVERSE SECTION				
Lamina	bowed	flat	bowed	bowed
Adaxial furrows	deep	slight	deep	moderate
Groove on midvein	present	absent	present	present
Number of 1° vascular bundles	2	4	3	3
Tangential bundle sheath cell walls	straight	rounded	rounded	rounded
Interruption of 1° vascular bundle sheaths	narrow	narrow	wide	wide/narrow
Number of 3° bundle sheath cells	10 – 12	9 – 10	7 – 8	7 – 9
1° bundle girder structure	abaxial	I-beam	I-beam	I-beam
2° bundles	absent	present	present	present
Number of bulliform cells	1 – 2	2 – 3	3 – 5	3 – 6
Bulliform cell shape	irregular	fan	fan	fan
Macrohairs	absent	absent	present	present
EPIDERMIS				
Subsidiary cell shape	triangular†	triangular†	dome	dome
Long-cells degree sinuous	strongly	slightly	strongly	strongly
Sinuous walls	wavy	wavy	wavy	wavy
Intercostal short-cells 1) irregularly placed, 2) in well defined rows	1	1	1	1
Bicellular microhair shape	clavate	elongate	clavate	clavate
Bicellular microhair length (μm)	33 – 38	20 – 25	34 – 40	25 – 38
Macrohairs on abaxial surface	absent	absent	absent	absent
Macrohairs on adaxial surface	absent	absent	absent	absent
Silica-bodies relatively	small	small	large	moderate
Silica-bodies alternate with	short-cells	short/long-cells	long-cells	short/long-cells

A slash(/) indicates presence of both character states.
† Dome subsidiary cells also present.

TAXONOMIC INTERPRETATION

A summary of the diagnostic characters of leaf anatomy for each species is presented in Table 2. Results suggest that seven distinct taxa exist based on anatomical characters. *Muhlenbergia plumbea* can be separated from the other species in the complex on many characters. It does not appear to have any close affinity with this complex and is probably more closely related to *M. uniflora* (Muhl.) Fernald or *M. arizonica* Scribn. as suggested by Soderstrom (1967). *Muhlenbergia fastigiata* and *M. utilis* are easily distinguishable from the other species of the complex by the position of the sclerenchyma in transverse section and the rows of short-cells on the epidermis. There were no differences in the leaf anatomy of *M. richardsonis* and *M. squarrosa* in either transverse section or surface view. This supports floristic treatments which have placed these two taxa in synonymy

(Cronquist et al. 1977, Hitchcock 1951). Although there are no outstanding characteristics of the other species, they can be readily identified by anatomical characteristics.

Muhlenbergia villiflora and *M. villosa* were similar anatomically. Differences were the nature of the outer tangential wall of the parenchyma sheath and the size of the silica-bodies on the abaxial epidermis. In the latter character, there was some variation in the dimensions of the cell. However, the silica-bodies of *M. villiflora* tend to be larger than those of *M. villosa*. Ellis (1976) reported that short-cells lack variation in size. To the extent that the shape and size of short-cells is constant, they can be reliable for taxonomic purposes. Hence, although the size of silica bodies for different species may overlap at the extremes, the tendency for silica-bodies of *M. villiflora* to be larger with some overlap does not preclude this species from being distinguishable from *M. villosa* anatomically.

ACKNOWLEDGMENTS

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MASON, JR., C.T. and P.B. Mason 1987. A handbook of Mexican roadside flora. 380 pp., illus. University of Arizona Press, 1615 E. Speedway, Tucson, AZ 85719. ISBN 0-8165-0997-2. Paper, $19.95.

The handbook includes "a brief overview of Mexico's geography and vegetation, a plant identification key preceding the account of species, and an illustrated glossary."

WARREN, B. and A. SPEER. 1987. Wilderness walkers: Naturalists in early Texas. 104 pp., illus.. Hendrick-Long Publishing Company, P.O. Box 25123, Dallas, TX 75225. ISBN 0-937460-26-5. Hbk, $12.95.

A book for the young naturalist with stories of seven early Texas scientists. Contents: Preface, Jean Louis Berlandier, Thomas Drummond, Ferdinand Jacob Lindheimer, Charles Wright, John James Audubon, Ferdinand Roemer, Gideon Lincecum, Time Line, Five who also came, Author's notes, Glossary, Suggested reading, Where to see collections made by early Texas Naturalist, About the Author-artist, About the researcher. A well done book that will prick the interest of any youngster with a love for nature.

CUSCUTACEAE OF LOUISIANA

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ABSTRACT

There are nine species of *Cuscuta* attributed to Louisiana. Three others are expected. This treatment includes keys, description of taxa, names of hosts, phenology, drawings of flowering and fruiting materials of 12 species, distribution maps for nine species, and a new varietal name combination.

INTRODUCTION

The genus *Cuscuta* has been included in the family Convolvulaceae (Bentham 1876; Peter 1894; Wilson 1960; Correll and Johnston 1970; Austin 1981; Correll and Correll 1982). However, in some of the more recent treatments of this genus (Hutchinson 1959; Takhtajan 1980; Cronquist 1981; Austin 1986), it is segregated from the Convolvulaceae and elevated to the rank of a monogeneric family, Cuscutaceae. Some distinctive features of this genus such as parasitic habit, imbricate corolla lobes (commonly contorted in Convolvulaceae), functioning of the primary archesporial cell directly into megaspore mother cell (in Convolvulaceae, the archesporial cell generally divides into a parietal cell and a primary sporogenous cell), persistence of one of the synergids (Tiagi 1951), general occurrence of acotyledonous coiled embryo, and absence of internal phloem support its separation from the Convolvulaceae.

Several contributions have been made to the understanding of the cytology (Fogelberg 1938; Raghavan 1957; Manitz 1983), haustorium formation (Tsivion 1979), morphology (MacPherson 1921; Smith 1934; Tiagi 1951, 1966; Narayana 1956; Pazourek 1958; Fujita 1964; Govil and Lavania 1980; Sampathkumar 1982), and seed germination (Gaertner 1950) of *Cuscuta*.

SIDA 12(2):361 – 379. 1987.

Yuncker (1932, 1965) directly or indirectly mentioned Louisiana for the distribution range of *C. cephalanthi*, *C. compacta*, *C. coryli*, *C. cuspidata*, *C. gronovii* var. *gronovii* and var. *calyptrata*, *C. indecora*, *C. obtusiflora* var. *glandulosa*, *C. pentagona*, and *C. umbellata*. The present treatment includes 12 species of *Cuscuta*. This study is based on Louisiana *Cuscuta* specimens (deposited in LAF, LSU, LTU, NATC, NLU, and NO) and Texas specimens (deposited in TAES). The description of each species is followed by its distribution within the United States. Specimen citations are provided for species with only one or two collection numbers. The names of host plants and flowering and fruiting period of *Cuscuta* refer to Louisiana specimens observed by the authors. Yuncker's *Cuscuta* illustrations are reproduced here from C. L. Lundell's "Flora of Texas."

SYSTEMATICS OF THE GENUS *CUSCUTA* L.

Dodder, Love vine, Angel's hair, Tangle gut, Strangle vine, Devil's gut, Witches' shoelaces

Plant body initially rooted upon germination, rootless after attaining parasitism; stem branched, filiform, twining, yellow-, pale-green-, or orange-colored, bearing numerous haustoria. Leaves, if present, scaly, initially distichous, becoming spiral with age. Laticifers (commonly known as translucent glandular cells in this genus) generally found in the midregion of bracts, sepals, and corolla lobes, and scattered on the fruits. Inflorescence of cymose clusters, these scattered on the stem and branches, compactly or loosely arranged. Flowers small, bisexual, regular, sessile to short-pedicelled, (3−)5-merous. Sepals almost distinct to the base or united to the middle or beyond, persistent. Corolla gamopetalous, campanulate, cylindrical, or rarely globose; lobes imbricate, spreading, ascending, or reflexed. Stamens equal to number of corolla lobes and alternating with them, epipetalous, exserted or occasionally sessile and included; anthers 2-celled; pollen smooth-walled. Antestaminal scales usually present at the base of corolla, generally reaching filaments, mostly united about the middle and forming a ridge at the base of corolla; the free margins and apex of scales generally fringed. Ovary superior, bicarpellary, bilocular, with two axile ovules in each locule; styles two and somewhat unequal (in ours), usually exserted from a style aperture; stigmas capitate (in ours). Fruit a circumscissile or irregularly dehiscing capsule, or indehiscent, 1- to 4-seeded, often surrounded by the persistent chartaceous withered corolla, variable in shape: ovoid, globose, oblate, or flask-shaped.

The size of the stem varies markedly in some species. The occurrence of pale-green-colored stems (chlorophyll and chloroplasts have been recorded)

suggests that this plant can be partially autotrophic. Kott (1959) reported the occurrence of multistage parasitism (i.e., secondary parasitism of *Cuscuta* plants on other cuscutas). Based on Lyshede's (1985) findings, the secretory structures that have been commonly known by the name "translucent glandular cells" are called here "laticifers." The presence of plasmodesmata between the haustoria and host cells is believed to assist the movement of food (Esau 1948). The inflorescence, sepals, petals, antestaminal scales, styles, and shape of the fruit provide the basis for classification. Although the stamens exhibit variations (Gandhi & Thomas 1983b), the antestaminal scales are the most significant structures in terms of floral evolution. The origin and morphology of scales have been disputed. Yuncker (1921), in his monograph of North American and West Indian species of *Cuscuta*, cited the morphological views of the following: Engelmann (scales are the dilations of the lowermost part of the filaments), Cunningham (scales are corolline in nature and are duplications of petals), Babington (scales are staminodes), and A. Braun (basically same view as that of Engelmann). Yuncker (1921) and Gandhi and Thomas (1983b) agreed with the views of Engelmann. Willis (1973) described the scales, as "5 scale-like staminodes alternating with stamens in base of corolla, often lobed or fimbriate." Basic chromosome number × = 7 or 15 (Cronquist 1981); 170 species (Willis 1973); although cosmopolitan, mostly American, especially in warmer parts (Cronquist 1981); about 48 species and more than 10 varieties found in USA (Soil Conservation Service 1982).

Yuncker (1965) recognized three subgenera and characterized them as follows:

CUSCUTA: styles distinct; stigmas linear.
GRAMMICA: styles distinct; stigmas mostly globose, capitate.
MONOGYNELLA: styles mostly united.

Following Yuncker, the 12 *Cuscuta* species from Louisiana are classified as indicated below:

Subgenus: GRAMMICA (Loureiro) Engelm.
Section: *Cleistogrammica* Engelm.
Subsection: *Platycarpae* Engelm.; e.g., *C. obtusiflora* and *C. polygonorum*
Subsection: *Arvenses* Yuncker; e.g., *C. pentagona*
Subsection: *Cephalanthae* Yuncker; e.g., *C. cephalanthi*
Subsection: *Indecorae* Yuncker; e.g., *C. coryli*, and *C. indecora*
Subsection: *Oxycarpae* Engelm.; e.g., *C. gronovii*
Subsection: Lepidanche Engelm.; e.g., *C. compacta*, *C. cuspidata*, *C. glomerata*, and *C. squamata*

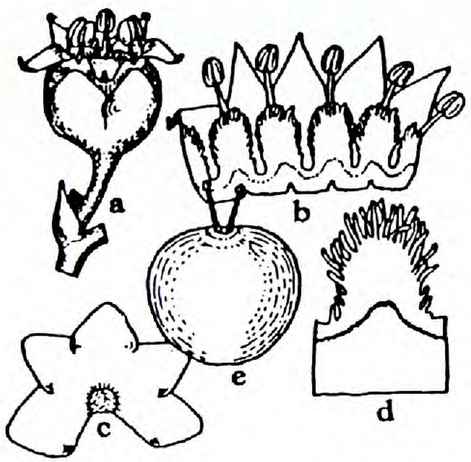
Section: *Grammica* Yuncker ("*Eugrammica*") Subsection: *Umbellatae* Yuncker; e.g., *C. umbellata*

KEY TO *CUSCUTA* IN LOUISIANA

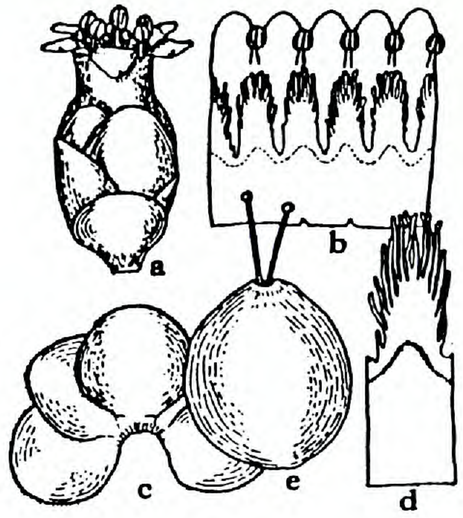
1	Flowers subtended by 1 – 10 bracts, often congested, sessile or subsessile; sepals almost distinct to the base 2
1	Flowers ebracteate (but cymose branches sometimes bracteate), loosely arranged, pedicelled; sepals united to various degrees 5
2(1)	Bract apex reflexed or spreading . . . . . *C. glomerata*
2	Bract apex erect 3
3(2)	Pedicels 0.5 – 3 mm long; flowers in loose panicles, not forming rope-like cymose clusters . . . . . *C. cuspidata*
3	Pedicels absent; flowers compactly arranged, forming rope-like cymose segments 4
4(3)	Bracts, sepals, and corolla lobes obtuse . . . . . *C. compacta*
4	Bracts and sepals acute; corolla lobes abruptly acute, acuminate, or minutely cuspidate . . . . . *C. squamata*
5(1)	Flowers mostly 3- or 4-merous; corolla lobes acute; antestaminal scales often bifid, scarcely fringed . . . . . *C. polygonorum*
5	Flowers mostly 5-merous, if 4-merous then corolla lobes obtuse and/or antestaminal scales profusely fringed at the apex 6
6(5)	Capsule circumscissile; calyx lobes abruptly acute-acuminate; corolla lobes acute-acuminate, reflexed, longer than the corolla tube . . . . . *C. umbellata*
6	Capsule not circumscissile; calyx and corolla lobes variously shaped and arranged, but not in the above combination 7
7(6)	Corolla lobe apex obtuse, if rarely subacute then style bases thickened 8
7	Corolla lobe apex acute to acuminate, inflexed; style bases not thickened 10
8(7)	Flowers mostly 4-parted; scales scarcely fringed; withered corolla crowning the capsule . . . . . *C. cephalanthi*
8	Flowers mostly 5-parted; scales profusely fringed at least at the apex; withered corolla about the base surrounding (rarely crowning) the capsule 9
9(8)	Calyx equalling or enclosing the corolla tube; styles diverging, mostly under 1 mm long . . . . . *C. obtusiflora*
9	Calyx shorter than the corolla tube; styles usually erect, to 1.8 mm long . . . . . *C. gronovii*
10(7)	Flowers generally smooth; ovary ovoid or globose . . . . . *C. pentagona*
10	Flowers fleshy, papillate; ovary flask-shaped 11
11(10)	Flowers mostly 4-merous; scales reduced, bifid or toothed, occasionally attached to filaments on either side . . . . . *C. coryli*
11	Flowers 5-merous; scales conspicuous, profusely fringed, free from stamens . . . . . *C. indecora*

1. CUSCUTA CEPHALANTHI Engelm., Amer. J. Sci. Arts 43:336. 1842. Fig. 1.

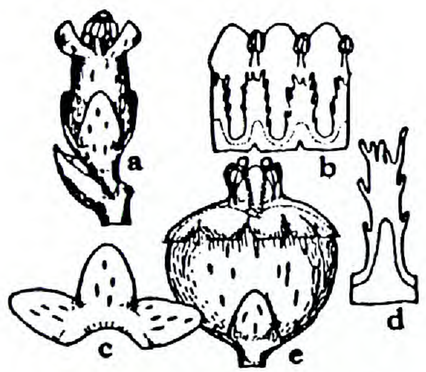
Stems smooth. Flowers about 2 mm long from the base of the flower to the corolla sinuses, 3- or 4-parted, or rarely 5-parted, with numerous



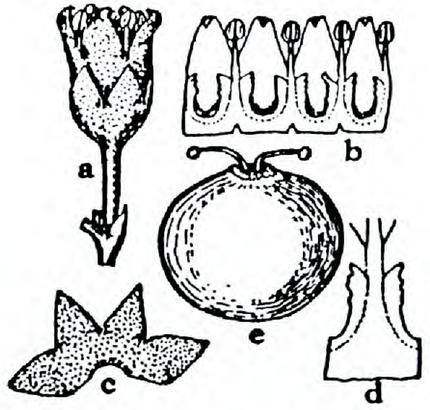
Cuscuta campestris Yuncker
a, flower, ×5; b, opened corolla, ×5; c, opened calyx, ×5; d, infrastamineal scale, ×10; e, matured capsule, ×5.



Cuscuta compacta Juss.
a, flower, ×5; b, opened corolla, ×5; c, opened calyx, ×5; d, infrastamineal scale, ×10; e, matured capsule, ×5.



Cuscuta Cephalanthi Engelm.
a, flower, ×5; b, opened corolla, ×5; c, opened calyx, ×5; d, infrastamineal scale, ×10; e, matured capsule, ×5.



Cuscuta Coryli Engelm.
a, flower, ×5; b, opened corolla, ×5; c, opened calyx, ×5; d, infrastamineal scale, ×10; e, matured capsule, ×5.

FIG. 1. From T. G. Yuncker in C. L. Lundell, Flora of Texas 3:123 – 150. 1943.

pellucid gland-like cells, sessile or subsessile in spicate or paniculately cymose clusters, the clusters at first open but soon becoming compact as the capsules mature. Calyx shorter than the corolla tube, deeply divided; lobes oblong-ovate, obtuse, slightly overlapping at the base, the margins often minutely irregular. Corolla tube cylindric-campanulate, soon enlarging about the maturing capsule; lobes much shorter than the tube, ovate, obtuse, erect to spreading. Stamens nearly as long as or somewhat shorter than the corolla lobes, sometimes attached in the sinus; filaments stout and more or less subulate, about equal to the oval or rounded anthers. Scales oblong, narrow, about reaching the filaments, bifid, fringed with scattered processes, bridged below the middle. Styles slender, about equal to or slightly longer than the usually somewhat oblate, rarely ovoid ovary; stigmas capitate. Capsule oblate or globose, capped by the withered corolla (adapted from Yuncker 1965).

Almost throughout USA; expected in Louisiana.

2. Cuscuta compacta Juss. ex Choisy, Mem. Soc. Phys. Hist. Nat. Geneve 9:281. 1841. Figs. 1, 6.

Stems coarse. Flowers sessile, arranged in compact glomerules, these forming rope-like segments. Bracts 4 – 10, subtending each flower, ascendingly imbricate, appressed, similar to sepals, tending to be keeled. Sepals free almost to the base, broadly ovate, obtuse, somewhat hooded at apex, scarcely fringed or serrulate, imbricate, to 3 mm long and 3.2 mm wide. Corolla cylindrical, constricted above the ovary, to 4.2 mm long; lobes triangular-oblong, obtuse, spreading or reflexed, to 1 mm long and 1.2 mm wide, apices incurved. Filaments to 0.5 mm long; anthers to 0.6 mm long. Scales united below the middle, fimbriate along the margins and apex, to 3 mm long. Style to 1 mm long; style aperture somewhat thickened. Capsule ovoid or slightly conic, often crowned with the withered corolla, to 4 mm long and 4.5 mm wide.

Eastern USA, and westward to Missouri, and Texas. Hosts: *Acer, Alnus, Ampelopsis, Apios, Aster, Baccharis, Bignonia, Boehmeria, Campsis, Carpinus, Cephalanthus, Cyrilla, Diospyros, Elephantopus, Eupatorium, Gelsemium, Halesia, Hypericum, Ilex, Itea, Iva, Lespedeza, Leucothoe, Ludwigia, Myrica, Nyssa, Rubus, Sambucus, Sapium, Sassafras, Saururus, Smilax, Vaccinium, Viburnum*. (July-) September - October (- November).

3. Cuscuta coryli Engelm., Amer. J. Sci. Arts 43:337. 1842. Fig. 1.

Stems smooth. Flowers fleshy, papillate, mostly 1.5 – 2 mm long from the base of the flower to the corolla sinuses, 4- or less frequently 5-parted, on pedicels shorter or longer than the flowers, in cymose-paniculate

clusters, in some specimens the flowers originate endogenously in the region of the haustoria and form dense, glomerulate clusters about the stem of the host. Calyx lobes about as long as the corolla tube, triangular-ovate, acute, scarcely overlapping at the base. Corolla tube cylindric-campanulate; lobes about as long as the tube, ovate-lanceolate or somewhat triangular-ovate, upright, the margins crenulate, the tips acute, inflexed. Stamens nearly as long as the corolla lobes; filaments stout and somewhat subulate, longer than the ovoid anthers. Scales mostly represented by toothed wings on either side of the filament attachment, rarely free, bridged below the middle. Ovary globose-ovoid, thickened about the interstylar aperture; styles slightly subulate, mostly about as long as the ovary; stigmas capitate. Capsule globose or oblate, the interstylar aperture comparatively large, the withered corolla about the upper part, eventually splitting and falling off (adapted from Yuncker 1965).

Eastern, central, and southwestern states; expected in Louisiana.

4. CUSCUTA CUSPIDATA Engelm., Boston J. Nat. Hist. 5:224. 1845. Figs. 2, 5.

Stems smooth. Flowers in loose panicled cymes. Pedicels 0.5 – 3 mm long. Bracts 1 – 5, similar to sepals but smaller. Sepals free nearly to the base, ovoid, suborbicular, or rhomboid-elliptic, acute, acuminate, or obtuse and minutely cuspidate, fringed, serrulate, or entire, to 2.2 mm long and 2 mm wide, appearing bluntly keeled. Corolla funnelform in outline, but bulbous at the base, 3 – 4.5 mm long; lobes oblong or ovate-lanceolate, obtuse, acute, or occasionally minutely cuspidate, erect, spreading, or reflexed, to 1.7 mm long and 1.2 mm wide, apices often incurved. Filaments to 0.7 mm long; anthers to 0.8 mm long. Scales united at or below the middle, fimbriate along the margins and apex, to 2.2 mm long. Style to 2.2 mm long; style aperture scarcely thickened. Capsule oblate or slightly conical, surrounded by or crowned with the withered corolla, to 2 mm long and 1.7 mm wide.

Most parts of USA (excluding NE and NW states, and California). Hosts: *Ambrosia*, *Baccharis*, *Eclipta*, and *Iva*.

5. CUSCUTA GLOMERATA Choisy, Mem. Soc. Phys. Hist. Nat. Geneve 9:280. 1841. Figs. 2, 5.

Similar to *C. compacta* in appearance, forming rope-like inflorescence segments wound tightly about the host stem. Flowers sessile, yellow. Bracts 3 – 6, similar to sepals in appearance but narrower, sometimes longer, bluntly keeled; margins not overlapping; apices acute to acuminate, spreading or recurved. Sepals distinct to the base, narrowly

rhomboid, acute, serrulate, to 4.7 mm long and 2.5 mm wide; margins often overlapping; apices spreading but not recurved. Corolla cylindrical except for the bulbose base, to 6 mm long; lobes oblong or triangular-lanceolate, acute or minutely cuspidate, spreading or reflexed, to 1.7 mm long and 0.8 mm wide, apices sometimes incurved. Filaments to 1 mm long; anthers to 0.8 mm long. Scales oblong, united at or above the middle, fringed at the apices, to 3.5 mm long. Ovary flask-shaped; style to 3.5 mm long. Capsule generally flask-shaped, crowned with the withered corolla.

Minnesota, Indiana, southward to Mississippi, Louisiana, and westward to North Dakota, South Dakota, Nebraska, Kansas, and Texas. Louisiana. Tangipahoa Parish: boggy field 2 mi N of Robert and US 190 on La 445, Sec. 13, T6S, R9E, 4 Sep 1980, *Tolley s.n.* (LSU). Host: *Helianthus angustifolius*.

6a. Cuscuta gronovii Willd. ex J.A. Schultes var. gronovii, Syst. 6:205. 1820. Figs 2, 6.

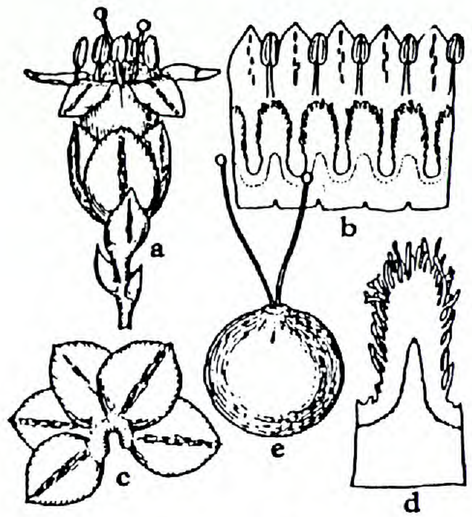
Stems occasionally coarse. Flowers arranged in loose or dense panicled cymes, ebracteate. Pedicels 0.5 – 4 mm long. Sepals ovate, ovoid, or suborbicular, obtuse, generally entire, rarely serrulate, united below the middle, overlapping, to 1.7 mm long and 1.5 mm wide. Corolla campanulate or globose, 3.5 – 5 mm long; lobes ovate, obtuse, spreading or reflexed, to 1.5 mm long and 1.5 mm wide. Filaments to 1 mm long; anthers to 0.7 mm long. Scales oblong, profusely fringed, united below the middle, 2.2 – 3 mm long. Style aperture scarcely thickened; styles 1.5 – 2 mm long, bases thickened. Capsule globose or conical, surrounded by or crowned with the withered corolla, to 4 mm wide.

The most common and abundant taxon of *Cuscuta* in North America and also extremely variable (Yuncker 1932); eastern USA, central states, and extending to Arizona. Hosts: *Ampelopsis, Aster, Bignonia, Boehmeria, Callicarpa, Campsis, Cephalanthus, Chrysopsis, Commelina, Croton, Elephantopus, Eupatorium, Ipomoea, Lactuca, Lonicera, Lycopus, Melia, Mikania, Perilla, Phytolacca, Polygonum, Rhus, Rubus, Salix, Sambucus, Solidago, Trachelospermum, Vernonia*, and *Vitis*. (June-) September-November.

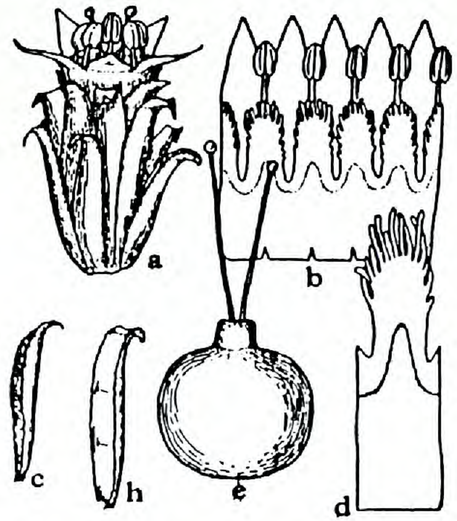
6b. Cuscuta gronovii var. calyptrata Engelm., Trans. Acad. Sci. St. Louis 1:508. 1859. Figs. 2, 6.

Characterized with serrate calyx lobes, longer corolla (ca 5 mm long), and capsule crowned with the withered corolla (fide Yuncker 1932).

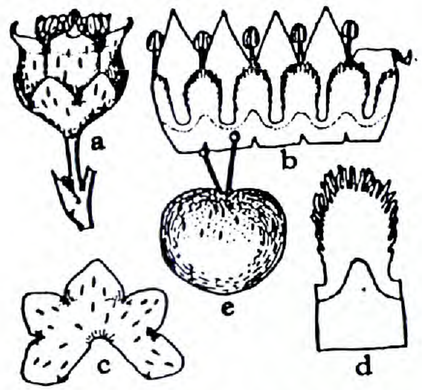
Texas and Louisiana.



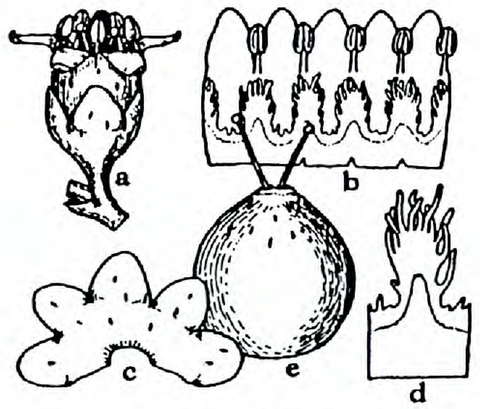
Cuscuta cuspidata Engelm.
a, flower, ×5; b, opened corolla, ×5; c, opened calyx, ×5;
d, infrastamineal scale, ×10; e, matured capsule, ×5.



Cuscuta glomerata Choisy
a, flower, ×5; b, opened corolla, ×5; c, calyx segment, ×5;
d, infrastamineal scale, ×10; e, matured capsule, ×5; h, bract, ×5.



Cuscuta glabrior (Engelm.) Yuncker
a, flower, ×5; b, opened corolla, ×5; c, opened calyx, ×5;
d, infrastamineal scale, ×10; e, matured capsule, ×5.



Cuscuta Gronovii Willd.
a, flower, ×5; b, opened corolla, ×5; c, opened calyx, ×5;
d, infrastamineal scale, ×10; e, matured capsule, ×5.

FIG. 2. From T. G. Yuncker in C. L. Lundell, Flora of Texas 3:123 – 150. 1943.

7. CUSCUTA INDECORA Choisy, Mem. Soc. Phys. Hist. Nat. Geneve 9:278. 1841. Figs. 3, 6.

Stems smooth or coarse. Flowers in panicled cymes, loosely or subcompactly arranged, fleshy, papillate, ebracteate. Pedicel 2–5 mm long. Sepals ovate or broadly rhomboid, obtuse-acute, united below the middle, slightly overlapping, to 1.5 mm long and 1.5 mm wide. Corolla campanulate, to 4.5 mm long; lobes triangular-ovate, acute to acuminate, spreading or ascending, to 1.5 mm long and 1.5 mm wide, apices incurved, forming a hood. Filaments to 0.7 mm long; anthers to 0.8 mm long. Scales profusely fringed, united below the middle, to 2 mm long. Ovary flask-shaped. Style aperture thickened; style to 1.7 mm long. Capsule globose, sometimes bluntly pointed at the apex, crowned with the withered corolla, to 4 mm wide.

Almost throughout USA. Hosts: *Agalinis*, *Aster*, *Baccharis*, *Borrichia*, *Chenopodium*, *Eupatorium*, *Helianthus*, *Heterotheca*, *Hypericum*, *Ipomoea*, *Iva*, *Kosteletzkya*, *Lepidium*, *Ligustrum*, *Myrica*, *Phragmites*, *Pluchea*, *Polygonum*, *Rhynchosia*, *Solidago*, *Suaeda*, *Tephrosia*, and *Vernonia*. (May-) July - October.

8. CUSCUTA OBTUSIFLORA H.B.K. var. GLANDULOSA Engelm., Trans. Acad. Sci. St. Louis 1:492. 1859. Figs. 3, 6.

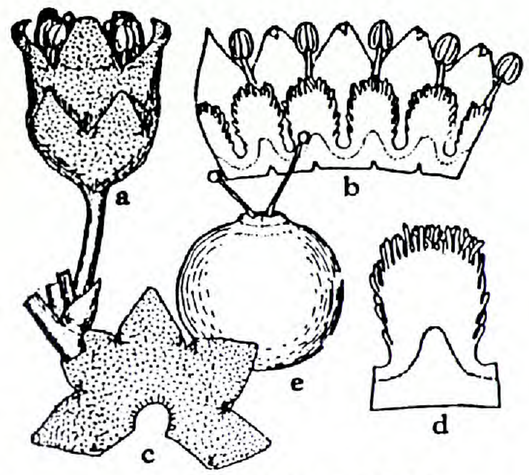
Stems smooth. Flowers loosely arranged in cymose clusters, often conspicuously glandular, 4- or 5-merous. Pedicel to 1.5 mm long. Sepals subequal or unequal, ovate, ovoid, or rhomboid, obtuse, united below the middle, to 2 mm long and 1.5 mm wide. Corolla campanulate, to 3 mm long; lobes triangular-ovate, obtuse-subacute, spreading or reflexed, to 1.3 mm long and 1.2 mm wide, apices generally erect, occasionally incurved. Filament to 0.6 mm long; anthers to 0.5 mm long. Scales truncate or bifid at the apex, conspicuously fringed at the apex, united below the middle, to 1.6 mm long. Styles diverging, to 1 mm long; base thickened. Capsule oblate, surrounded by the withered corolla at the base, to 3 mm wide.

Gulf States, extending westward to Texas and northward to eastern central states. Hosts: *Alternanthera*, *Hygrophila*, *Lythrum*, *Persicaria*, *Polygonum*, and *Xanthium*. July - September (-October).

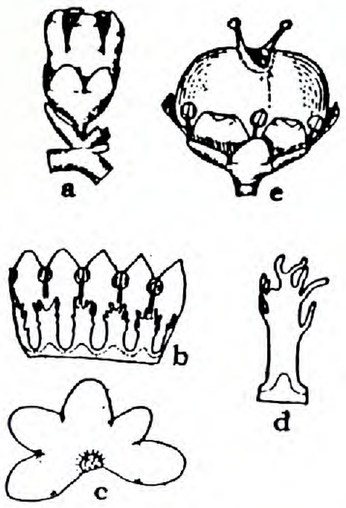
9. CUSCUTA PENTAGONA Engelm., Amer. J. Sci. Arts 43:340. 1842. Figs. 3, 6.

Capsule surrounded by the withered corolla to the middle; corolla not saccate; interstylar aperture inconspicuous ..... var. *pentagona*

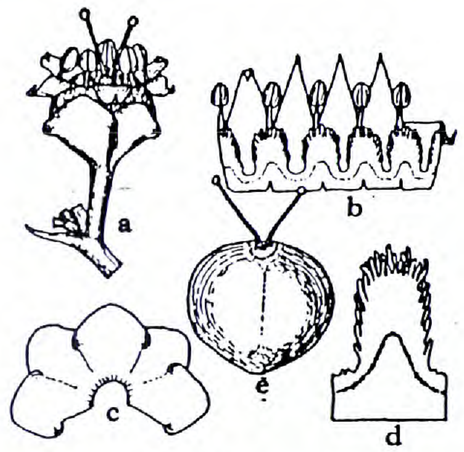
Capsule surrounded by the withered corolla for the most part; corolla often saccate in between the lines of stamen attachment; interstylar aperture conspicuous ..... var. *glabrior*



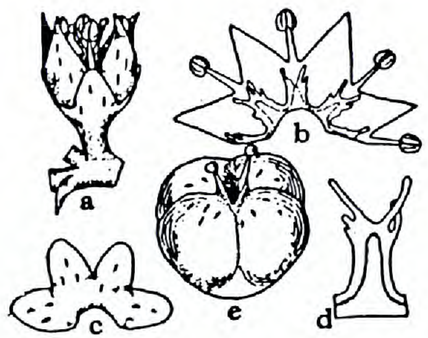
Cuscuta indecora Choisy
a, flower, ×5; b, opened corolla, ×5; c, opened calyx, ×5;
d, infrastamineal scale, ×10; e, matured capsule, ×5.



Cuscuta obtusiflora H.B.K. var. *glandulosa* Engelm.
a, flower, ×5; b, opened corolla, ×5; c, opened calyx, ×5;
d, infrastamineal scale, ×10; e, matured capsule, ×5.



Cuscuta pentagona Engelm.
a, flower, ×5; b, opened corolla, ×5; c, opened calyx, ×5;
d, infrastamineal scale, ×10; e, matured capsule, ×5.



Cuscuta Polygonorum Engelm.
a, flower, ×5; b, opened corolla, ×5; c, opened calyx, ×5;
d, infrastamineal scale, ×10; e, matured capsule, ×5.

FIG 3. From T. G. Yuncker in C. L. Lundell, Flora of Texas 3:123 – 150. 1943.

9a. CUSCUTA PENTAGONA var. PENTAGONA.

Cuscuta campestris Yuncker, Mem. Torrey Bot. Club 18(2):138. 1932.

Stems smooth. Flowers arranged in loose cymose clusters, ebracteate. Pedicel to 1.7 mm long. Calyx sometimes angled at the sinuses, to 1.6 mm long; lobes subequal or unequal, oblong, ovate, or rhomboid, obtuse, serrulate, to 1.5 mm wide. Corolla campanulate, to 2.5 mm long; lobes triangular-ovate, acute to acuminate, spreading or reflexed, to 1.2 mm long and 1 mm wide, apices incurved. Filaments to 0.6 mm long; anthers to 0.4 mm long. Scales fringed at apex, united below the middle, to 1.5 mm long. Style to 0.7 mm long. Capsule oblate, globose, or ovoid, surrounded by the withered corolla at the base, to 3 mm wide.

Almost throughout USA. Hosts: *Aster, Baptisia, Bidens, Boltonia, Broussonettia, Brunnichia, Campsis, Convolvulus, Dalea, Euphorbia, Helianthus, Lagenaria, Lespedeza, Oenothera, Persicaria, Polygonum, Polypremum, Solidago, Vitis*, and *Xanthium*. May - July (-September).

Yuncker characterized *C. pentagona* with angled calyx and its absence in *C. campestris*. It has been found that the angled calyx is not a constant feature; it is present in some flowers and absent in others, even within an individual. This was also observed by T. Beliz (University of California, Berkeley).

9b. CUSCUTA PENTAGONA var. **glabrior** (Engelm.) Gandhi, Thomas, & Hatch, comb. nov. *C. verrucosa* var. *glabrior* Engelm., Amer. J. Sci. Arts 43:341. 1842; *C. glabrior* (Engelm.) Yuncker, Mem. Torrey Bot. Club 18(2):140. 1932.

Cuscuta verrucosa Engelm., Amer. J. Sci. Arts 43:341. 1842, non Sweet 1823; *C. arvensis* var. *verrucosa* Engelm., Trans. Acad. Sci. St. Louis 1:495. 1859; *C. pentagona* var. *verrucosa* (Engelm.) Yuncker, Illinois Biol. Monogr. 6:142. 1921.

Stems smooth. Flowers often conspicuously papillate. Sepals united at or about the middle, triangular-ovate, obtuse-acute or abruptly acuminate, not overlapping. Corolla campanulate or subglobular, often saccate between the lines of stamen attachment. Capsule oblate, papillate at least at the apex, surrounded by the withered corolla for the most part; interstylar aperture conspicuous.

New Mexico to Louisiana. Cameron Parish: roadside, near east end of Rockfeller Wildlife Refuge, 23 Jun 1962, *J. W. Thieret* 8669 (NATC). Host: *Sesuvium*. Sometimes this taxon is mistaken for *C. umbellata* because of the separation of the fruit from the corolla (fide Yuncker 1965).

The name *C. verrucosa* Engelm. (1842) is illegitimate because it is a later homonym of Sweet (1823). However, according to Article 68.2 of

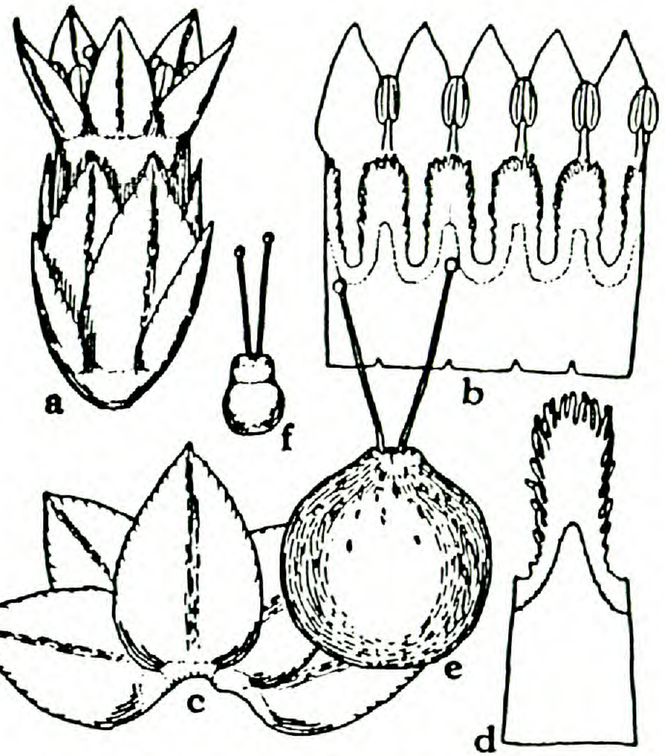
"International Code of Botanical Nomenclature" (1983), the name *C. verrucosa* var. *glabrior* is legitimate. As per the code Article 72 (Note 1), the name *C. arvensis* var. *verrucosa* is validly published, but does not involve any basionym or parenthetic author citation; hence, this name has priority from the year 1859. Although the name *C. pentagona* var. *verrucosa* is legitimate, its priority dates from Engelmann's legitimate 1859 usage, not from illegitimate 1842 usage. Therefore, at varietal rank, the epithet *glabrior* has priority, and a new combination is made here using the legitimate 1942 epithet *glabrior*.

10. CUSCUTA POLYGONORUM Engelm., Amer. J. Sci. Arts 43:342. 1842. Figs. 3, 5.

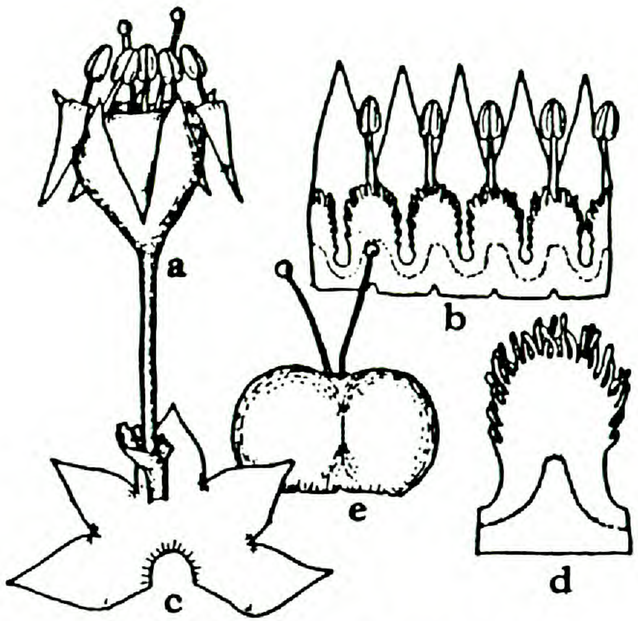
Stems smooth. Flowers arranged in compact cymose clusters, subsessile, ebracteate, mostly 3- or 4-merous. Sepals ovate, obtuse-subacute, not overlapping, united below the middle, unequal, to 1.5 mm long and 1.2 mm wide. Corolla campanulate, to 2.5 mm long; lobes triangular-ovate, acute to acuminate, ascending, to 1.5 mm long and 1.2 mm wide, apices incurved. Filaments 0.8 mm long; anthers 0.5 mm long. Scales hardly fringed, sometimes toothed and/or bifid at the apex, almost free to the base, to 1 mm long. Style aperture thick; style to 0.7 mm long, bases thickened. Capsule oblate, globose, or conical, to 1.2 mm long and 2.5 mm wide.

Eastern USA, extending westward to central states and Texas. Louisiana. East Baton Rouge Parish: along the Mississippi River at the jct of Stadium Drive and La 327 at Louisiana State University garbage dump, Baton Rouge, Secs. 61 and 65, T7N, R1W, 5 Oct 1981, *Thomas 78758* (NLU); and Ouachita Parish: along eastern bank of Ouachita River between levee and water at Louisville Ave. bridge in Monroe, 5 Sep 1979, *Thomas 67265* (NLU). Host: *Xanthium strumarium*.

According to MacRoberts (1984), Riddell (1852) reported the occurrence of *C. polygonorum* in Louisiana. Yuncker (1932, 1965) described the distribution of this species as follows: "New England and Ontario westward to Nebraska and Arkansas." Correll and Johnston (1970) added Texas to Yuncker's distribution data on the basis of Small (1933), but did not include Louisiana. Based on this account, Gandhi and Thomas (1983a) reported *C. polygonorum* as "new to Louisiana." MacRoberts mentioned that Riddell's collections, in part, are likely to be found in the US National Herbarium (US); however, a search was made for specimens of this species from Louisiana but were not located. T. Beliz (University of California, Berkeley; pers. comm. 1986), who is presently monographing *Cuscuta*, indicated that she has not found Riddell's specimen in any of the loan materials.



Cuscuta squamata Engelm.
a, flower, ×5; b, opened corolla, ×5; c, opened calyx, ×5;
d, infrastamineal scale, ×10; e, matured capsule, ×5; f, ovary, ×5.



Cuscuta umbellata H.B.K.
a, flower, ×5; b, opened corolla, ×5; c, opened calyx, ×5;
d, infrastamineal scale, ×10; e, matured capsule, ×5.

FIG. 4. From T. G. Yuncker in C. L. Lundell, Flora of Texas 3:123 – 150. 1943.

Parishes in Louisiana

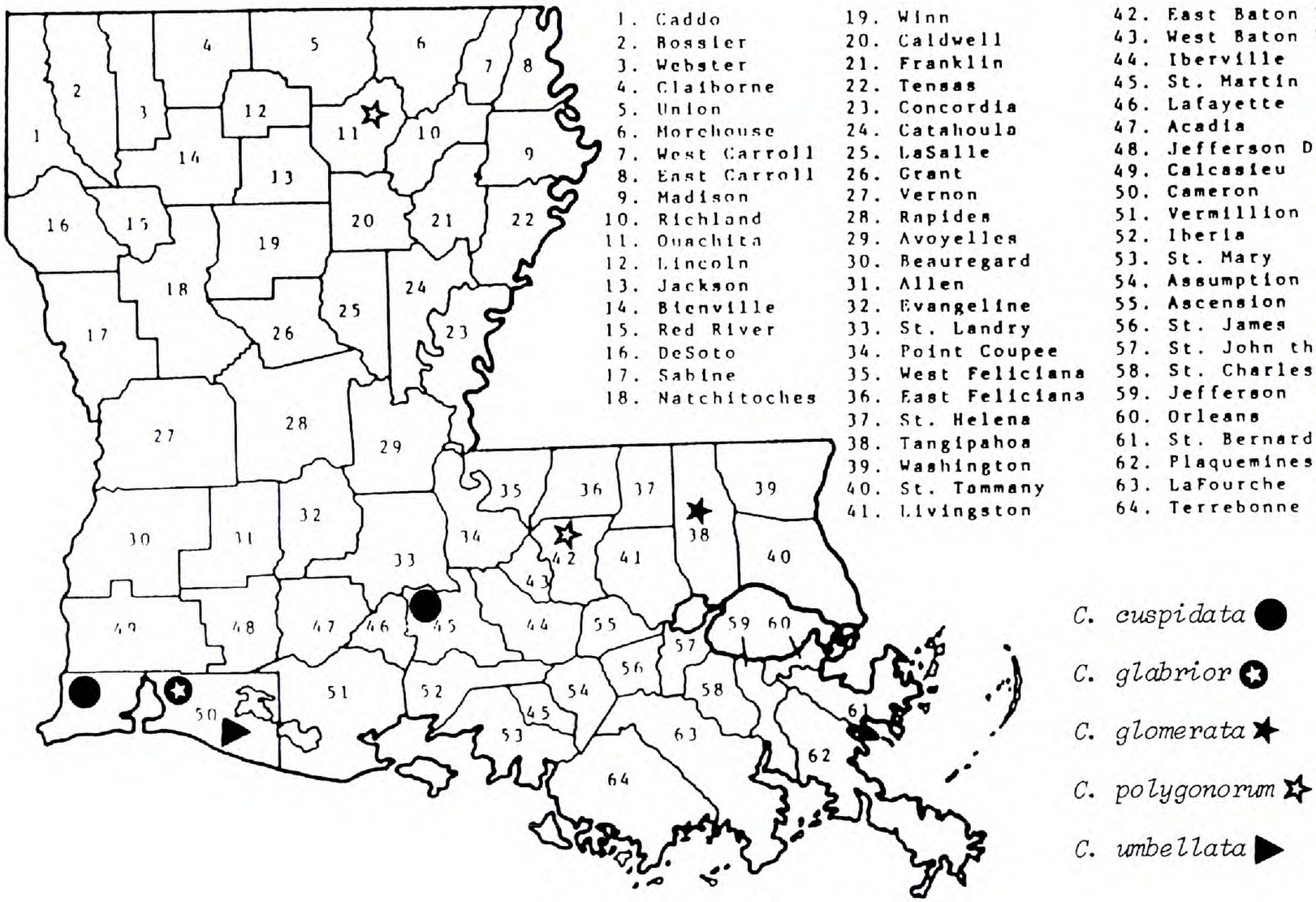
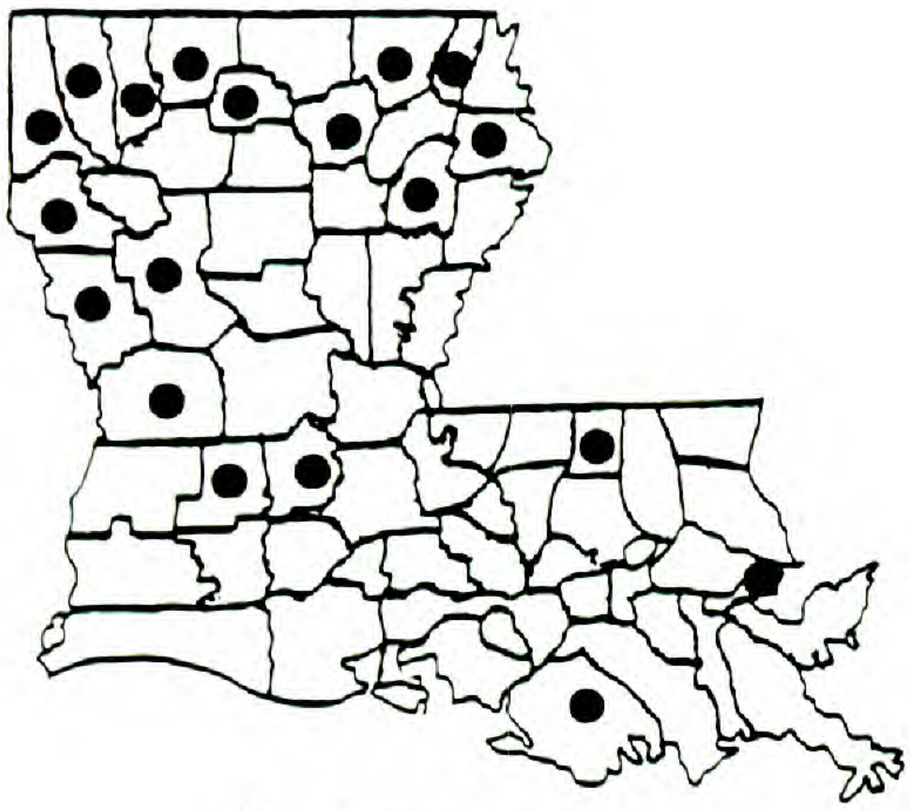
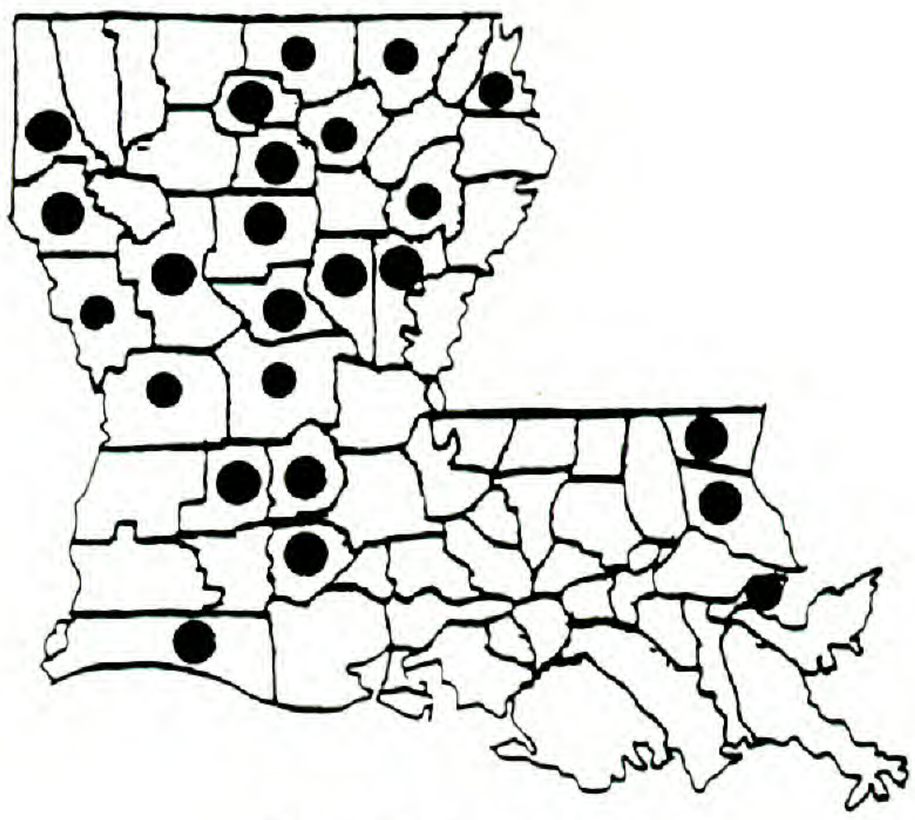


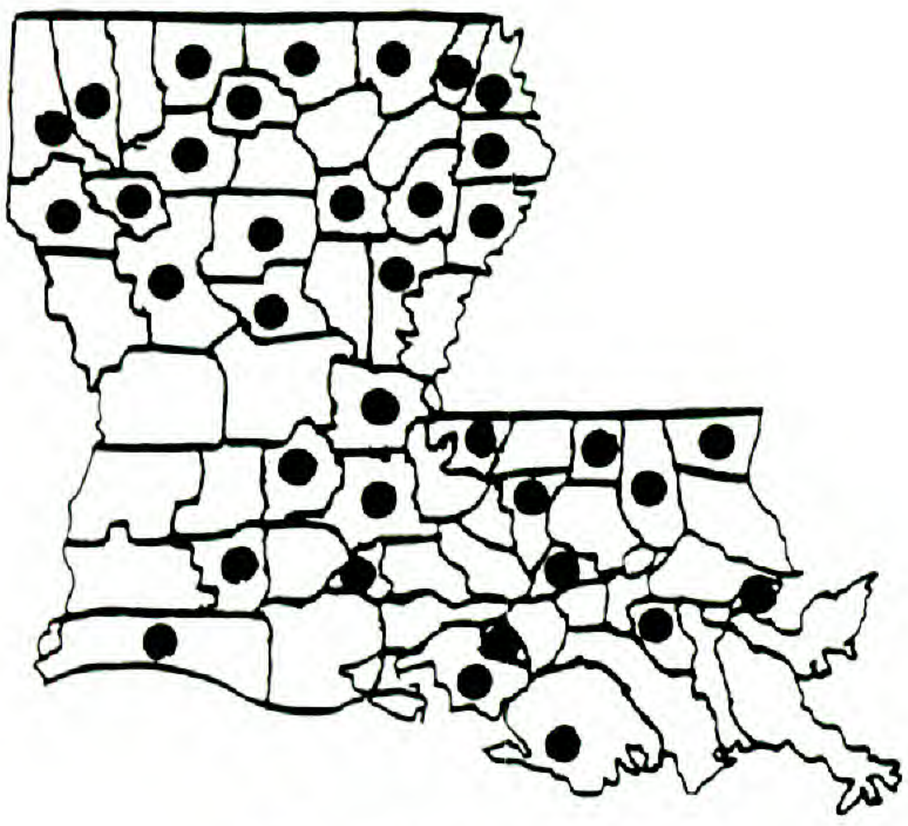
FIG. 5. Distribution of *Cuscuta* in Louisiana, I.



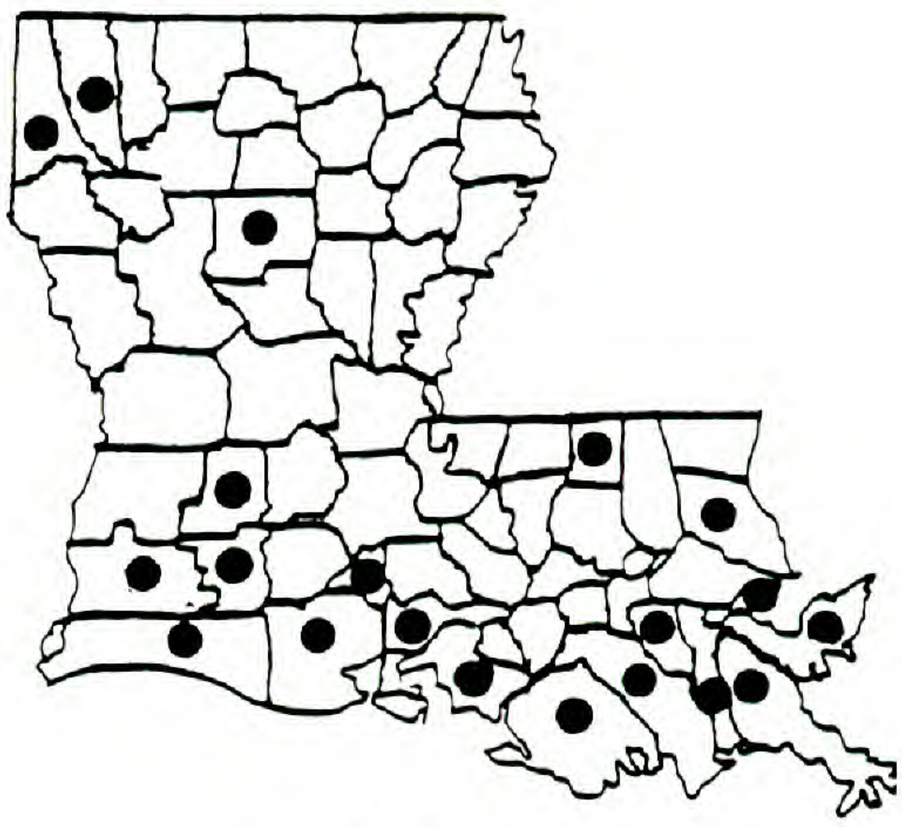
C. campestris



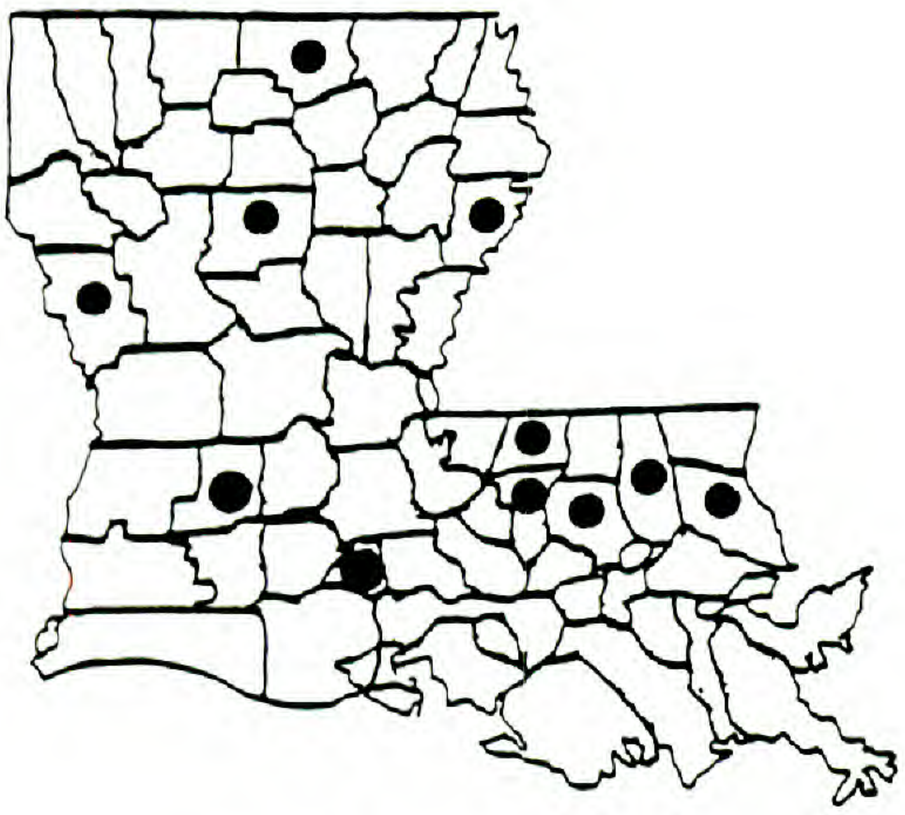
C. compacta



C. gronovii



C. indecora



C. obtusiflora

C. pentagona

FIG. 6. Distribution of *Cuscuta* in Louisiana, II.

11. Cuscuta squamata Engelm., Trans. Acad. Sci. St. Louis 1:510. 1859. Fig. 4.

Stems smooth or coarse. Flowers sessile, arranged in compact cymose clusters, these generally forming rope-like segments as in *C. compacta*. Bracts 3 – 6 subtending each flower, similar to sepals but smaller. Sepals almost distinct to the base, ovate, subacute to acute, to 3.5 mm long and 2.5 mm wide. Corolla cylindrical, to 5 mm long; lobes lanceolate, abruptly acute, acuminate, or minutely cuspidate, generally ascending, to 2.2 mm long and 1.1 mm wide, apices erect or incurved. Filaments to 0.7 mm long; anthers to 0.8 mm long. Scales fringed along the margins and apex, united below the middle, to 2 mm long. Style to 2.5 mm long. Capsule ovoid or ellipsoid.

New Mexico and Texas; expected in Louisiana because of its reported occurrence in southeastern Texas (Correll and Johnston 1970).

Although Overby (1974) reported the occurrence of *C. squamata* (*Overby 64*, 4 Sep 1972, NLU), the authors concluded that the specimen was misidentified, and was in fact *C. indecora*.

12. Cuscuta umbellata H.B.K., Nov. Gen. & Sp. Pl. 3:121. 1818. Figs. 4, 5.

Stems smooth. Flowers cream-, white-, or straw-colored, smooth or infrequently slightly papillate, arranged in loose or subcompact cymose umbels, commonly with some pellucid glandular cells. Pedicels 1 – 3 mm long. Calyx turbinate, to 2.5 mm long; lobes ovate, acuminate, united below the middle, overlapping, subequal, to 1.6 mm long and 1.6 mm wide. Corolla campanulate, to 4 mm long; lobes lanceolate, acute-acuminate, reflexed, to 2.4 mm long and 1.1 mm wide. Filaments to 0.8 mm long; anthers to 0.7 mm long. Scales spathulate, moderately fringed, united at the bases, to 1.5 mm long. Styles to 2.2 mm long; style aperture scarcely thickened. Capsule oblate, surrounded by withered corolla, generally circumscissile, to 2 mm long and wide.

Florida to California. Louisiana. Cameron Parish: marshy waste beside La 82, about 9.4 mi E of Grand Chenier, T15S, R4W, 16 Jun 1984, *Dutton 2267* and *Taylor 7437*. Hosts: *Acnida* and *Apios*.

ACKNOWLEDGMENTS

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Cuscuta illustrations from the Flora of Texas; Dr. Dan H. Nicolson (Smithsonian Institution) for helpful suggestions on the nomenclature, and the curators of the following herbaria for their cooperation: LAF, LSU, LTU, NATC, and NO. This is a co-operative contribution of the Biology Department of Northeast Louisiana University and the Texas Agricultural Experiment Station, College Station, T.A. No. 21875.

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CORRIGENDUM

VILLARREAL Q, J.A. 1987. *Coutaportla pailensis* (Rubiaceae), a new species from Coahuila, México. SIDA 12(1):223 – 225.

Page 223, seventh line, recently described *C. guatemalensis* Lorence 1986) should read recently proposed *C. guatemalensis* (Standley) Lorence.

Page 223, Latin diagnosis, first line, 4 – 12 cm longae should read 4 – mm longae; fourth line, Capsula oblonga 8 – 16 mm should read 8 – 10 mm.

Page 225, last line of last paragraph should end with: the medial placenta position and the arid habitat.

Acknowledgments: I want to thank Dr. Marshall C. Johnston for the Latin diagnosis and reading the manuscript, to Miguel A. Carranza for preparing the illustration and to Jorge Wehbe for showing me the locality.

THE SHALE BARREN ENDEMIC, *ARABIS SEROTINA* (BRASSICACEAE)

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ABSTRACT

A re-examination of *Arabis serotina* Steele shows that several morphological characters consistently correlate with the flowering time which clearly separates this species from its close relative, *Arabis laevigata* (Muhl.) Poir. var. *burkii* Porter. A chromosome count of 2n = 14 is reported. This information supports the original contention that *Arabis serotina* is a good morphological species.

INTRODUCTION

The name *Arabis serotina* was proposed by Edward Steele in 1911 to describe a species of mustard which he found near Millboro, Bath County, Virginia. This locality is centrally located within the mid-Appalachian shale barrens (Keener 1970, 1983). Steele, an astute observer of native habitats and their floras, originally coined the term "shale barren" to describe the distinctive, sparsely vegetated woodlands underlain by Devonian age shales. The reader is referred to Keener (1983) for information about this habitat and its endemic flora.

Arabis laevigata var. *burkii* is a plant described from dry hills of Pennsylvania (Porter 1890) and named for its discoverer, Isaac Burk. Variety *burkii* is distinguished by its cauline leaves lacking the auricles at the leaf base which characterize the typical variety. Both varieties are spring-flowering. Variety *burkii* appears to be a well-marked entity which occupies drier woodlands than variety *laevigata*. *Arabis serotina*, a mid- to late summer-flowering species, is a shale barren endemic whereas *A. laevigata* var. *burkii* occupies a variety of xeric habitats, including shale barrens, and ranges well north and west of the shale barren region.

Hopkins (1937), in his treatment of eastern and central North American species of *Arabis*, reduced *A. serotina* to synonymy under *A. laevigata* var. *burkii*. The two taxa bear a strong resemblance to one another and recent manuals treating the flora of the central Appalachians follow Hopkins. Despite this, the name *A. serotina* is used in recent floristic papers (Keener 1970, 1983) and among botanists familiar with the shale barren flora. This paper recognizes *Arabis serotina* as a good species and details its differences from *Arabis laevigata* var. *burkii*.

SIDA 12(2):381 – 389. 1987.

DISCUSSION

The most striking difference between *Arabis serotina* and *Arabis laevigata* var. *burkii* is flowering time which is fully two months apart even when the plants occupy similar sites in the same area. Besides this, the differences largely feature the habit of the plants. A number of measurements have been made to determine whether or not these differences correlate with flowering time. A quantitative analysis of the two is hindered by the paucity of specimens available for study and by the virtual absence of foliage on *A. serotina* at flowering time. The number was further reduced because individual specimens needed to be treated either as flowering or fruiting. Good flowering plants rarely have fully elongated, mature siliques and good fruiting plants often show reduced floral development. Because of this, flowering specimens could not be compared to fruiting specimens which effectively halved the number of specimens available for analysis in each category. The only character measured which does not overlap is calyx length but even this shows no obvious hiatus in the range of variation. Because so few specimens are available, graphical means are used to display the differences. Figure 1 differentiates the vernal-flowering plants from the summer-flowering ones based on calyx length and inflorescence width. Additional characters measured in this study are presented in Table 1 and comments made in the discussion following. Averages of measurements (fruiting specimens) for plant height, number of inflorescence branches, height of the lowest branch, and inflorescence width were used to generate an average plant of both *A. serotina* and *A.*

TABLE 1. Comparison of averages and ranges of selected morphological characters of *Arabis laevigata* var. *burkii* and *Arabis serotina*. (N = number of plants; calyx and siliques, 1 – 5 measurements per plant).

CHARACTER	ARABIS LAEVIGATA VAR. BURKII	ARABIS SEROTINA
Plant Height (cm)	41.07 (N = 53) (21.0 – 66.6)	52.81 (N = 13) (41.0 – 97.0)
Number of Branches	2.1 (N = 53) (0 – 9)	19.2 (N = 11) (3 – 41)
Height of Lowest Branch (cm)	11.33 (N = 53) (6.5 – 37.6)	24.40 (N = 9) (13.0 – 40.0)
Inflorescence Width (cm)	12.17 (N = 55) (7.0 – 21.2)	28.19 (N = 13) (22.0 – 40.0)
Calyx Length (mm)	3.83 (N = 18) (2.9 – 4.8)	2.55 (N = 18) (2.0 – 3.3)
Silique Length (cm)	7.62 (N = 39) (5.25 – 9.78)	5.76 (N = 14) (4.30 – 7.94)

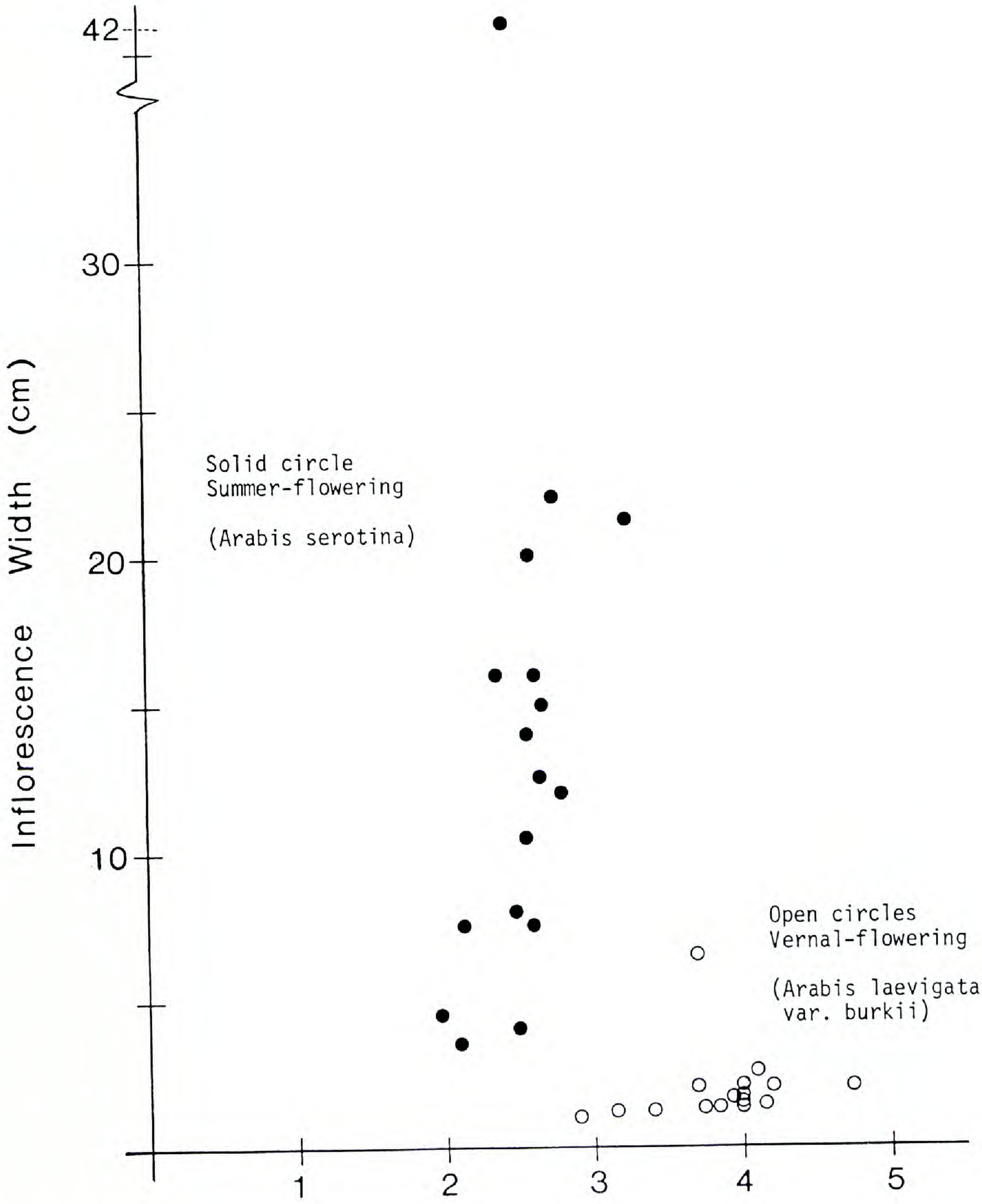

FIG. 1. Calyx length vs. inflorescence width for vernal-flowering *Arabis laevigata* var. *burkii* (open circles) and summer-flowering *Arabis serotina* (solid circles).

laevigata var. *burkii*. Drawn to scale, Figure 2 gives a visual representation of differences which numbers alone fail to impress. A brief discussion of the primary characters is appropriate.

Calyx Length: The calyx of *A. serotina* ranges from just less than 2.0 mm to 3.0 mm (one specimen to 3.26 mm). Porter's original diagnosis describes *A. laevigata* var. *burkii* as having flowers smaller than the typical variety. This seems to be generally true from my measurements but at least some specimens of var. *burkii* equal those of var. *laevigata*. The calyx of variety *burkii* begins at 3.0 mm (one flower measured 2.8 mm) and ranges

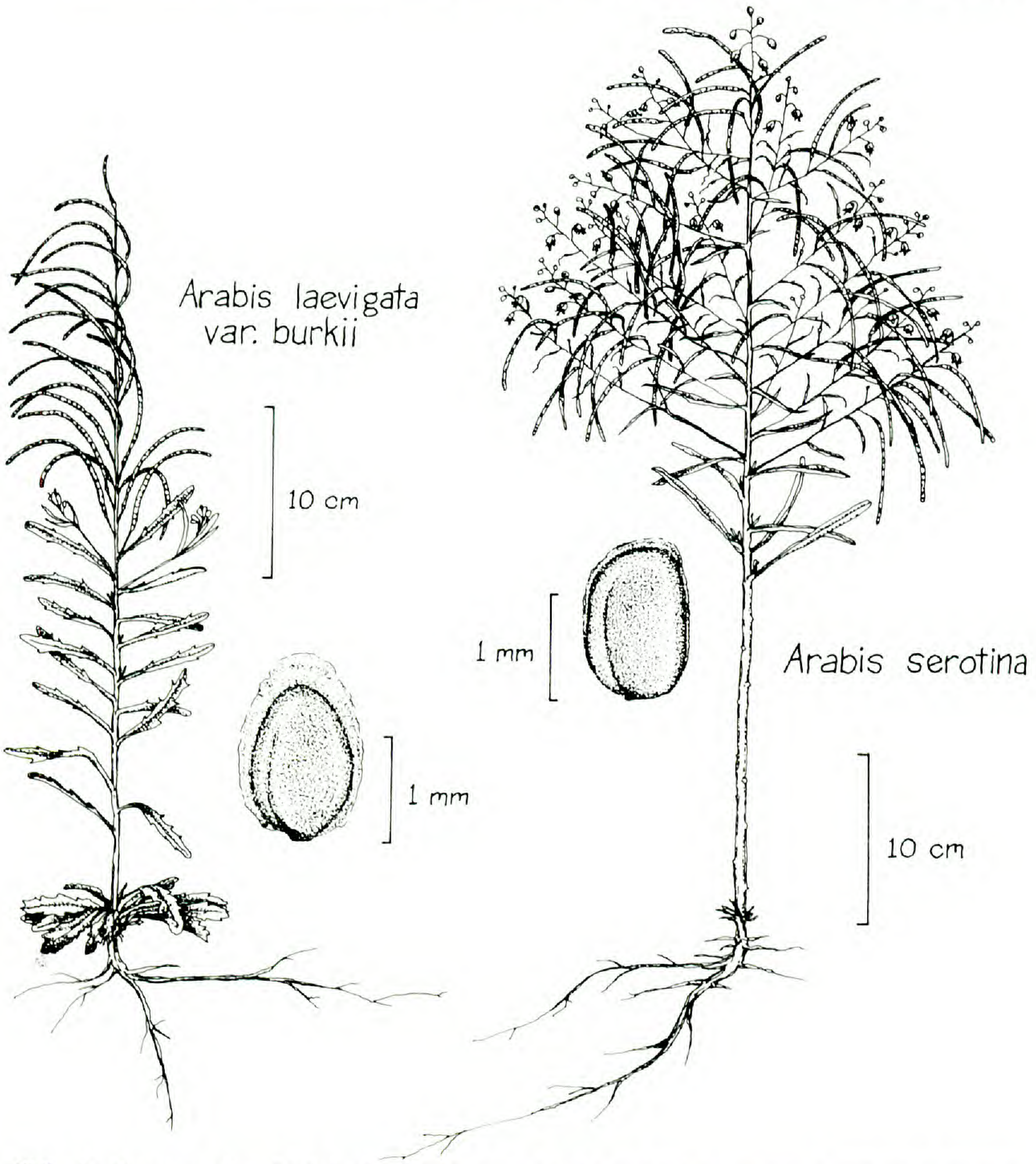

FIG. 2. "Average plants" of *Arabis laevigata* var. *burkii* and *Arabis serotina* based on characters presented in Table 1. Detail of seeds.

up to 5.0 mm. Average lengths from five different flowers per plant and 0.4 mm size classes are used to generate Figure 3. It is readily apparent that calyx lengths fall into two size ranges with the separation being at about 3.2 mm.

Inflorescence Width: This feature combines two differences in habit which normally separate the two entities. These are number of inflorescence branches and their configuration and development. *Arabis serotina* is a much-branched species with diffuse inflorescence. Although basically racemose on each branch, it commonly displays secondary

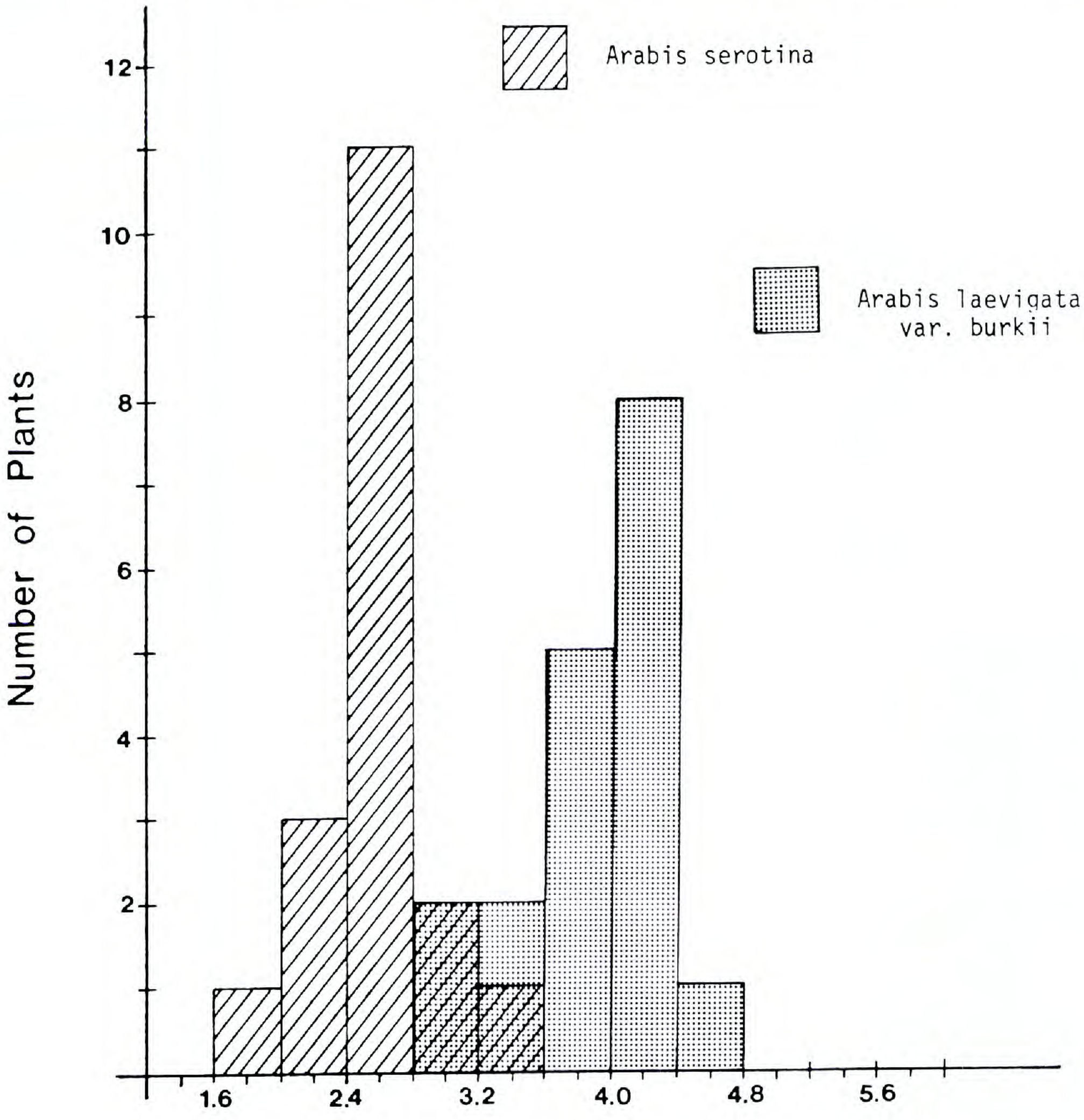

FIG. 3. Frequency distribution of mean calyx length (5 flowers per plant).

branching thereby attaining a paniculate appearance. *Arabis laevigata* var. *burkii* is simply racemose. A few strongly ascending lateral racemes are often present, or rarely numerous when the primary axis is damaged. Lateral branching is usually delayed and thereby noticeably later in fruit development than the primary axis. By contrast, the entire divergent inflorescence of *A. serotina* develops simultaneously.

Plant Height: Fully mature plants of *A. serotina* average somewhat larger than *A. laevigata* var. *burkii*. The latter may be very short when flowering commences and elongate rapidly but seldom attain a height greater than 0.5 m. By contrast, the summer-flowering *A. serotina* has reached considerable stature when anthesis begins. Although some plants may grow to only about 40 cm, many will reach 80 – 100 cm.

Flowering Time: *Arabis serotina* flowers from mid-July to September. By contrast, *A. laevigata* var. *burkii* and *A. laevigata* var. *laevigata* flower in April and May. The latter are early spring wildflowers which begin to bolt as the warmer season progresses. In more protected sites flowering can be expected to be advanced as on a shale barren where the southerly exposure has a considerable solar warming effect. With this consideration, fully eight to ten weeks can be expected to separate the final flowering of *A. laevigata* and the earliest flowering of *A. serotina*. As Steele pointed out, this alone is sufficient to separate the two at the species level. A population of *A. serotina* in Augusta County, Virginia, possessed well-developed flower buds in mid-June, 1985. Interestingly, a specimen from this population also had the longest calyces.

Seed Morphology: The seeds of *Arabis* are rounded to elliptic and winged by an outward extension of the seed coat (Murley 1951). The wing and seed dimensions are useful taxonomic characters. Seeds of *A. serotina* are larger, the body being narrowly elliptic, 1.5 – 2.0 times as long as broad and very narrowly winged, the wing being 0.1 – 0.2 mm wide or virtually obsolete. Seeds of *A. laevigata* var. *burkii* are smaller in the body and broadly elliptic, less than 1.5 times as long as broad but nearly as large when including the wing. The wing is 0.25 – 0.50 mm wide though exceptionally full-bodied seeds may be narrowed laterally. In the original description Steele reversed this stating that the seeds of *A. serotina* were more broadly winged. Seeds of *A. serotina* are more often yellowish brown whereas those of *A. laevigata* are reddish brown.

Silique Length: This character shows a great consistency within populations but considerable variation between populations. *Arabis serotina* generally has shorter siliques but populations with fruits near the upper part of the range (see Table 1) are not distinguishable from *A. laevigata* var. *burkii*.

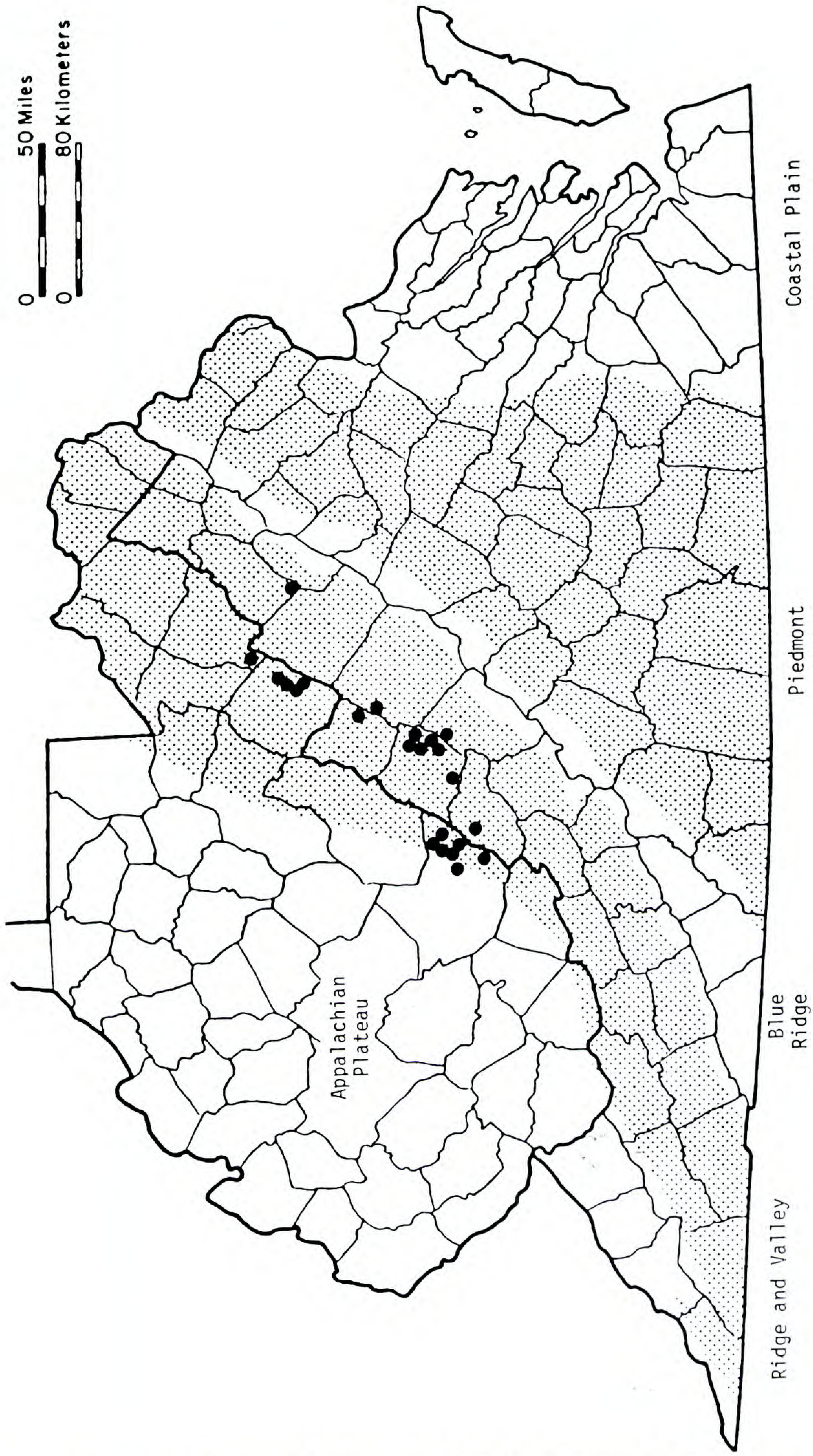

FIG. 4. Known distribution of *Arabis serotina*. Each dot represents a known population.

Chromosome Number: A count has not previously been made for *Arabis serotina*. From root tip preparation of germinating seeds, a $2n$ count of 14 was made. A count for *A. laevigata* var. *burkii* was not made as part of this study. Counts of $n = 7$ are reported for *A. laevigata* (variety unspecified) by Easterly (1963) and Kovanda (1978).

Range: Distributions of *Arabis serotina* and *A. laevigata* var. *burkii* are shown in Figures 4 and 5 respectively. Despite the fact that these two occupy similar habitats, their ranges appear to overlap only slightly in Pendleton and Hardy counties, West Virginia. Bartgis (1985) has shown that the two occupy different ranges within this portion of the shale barren region occurring together at only two sites. Sites in Greenbriar County West Virginia, and Shenandoah County, Virginia, are slightly disjunct. In

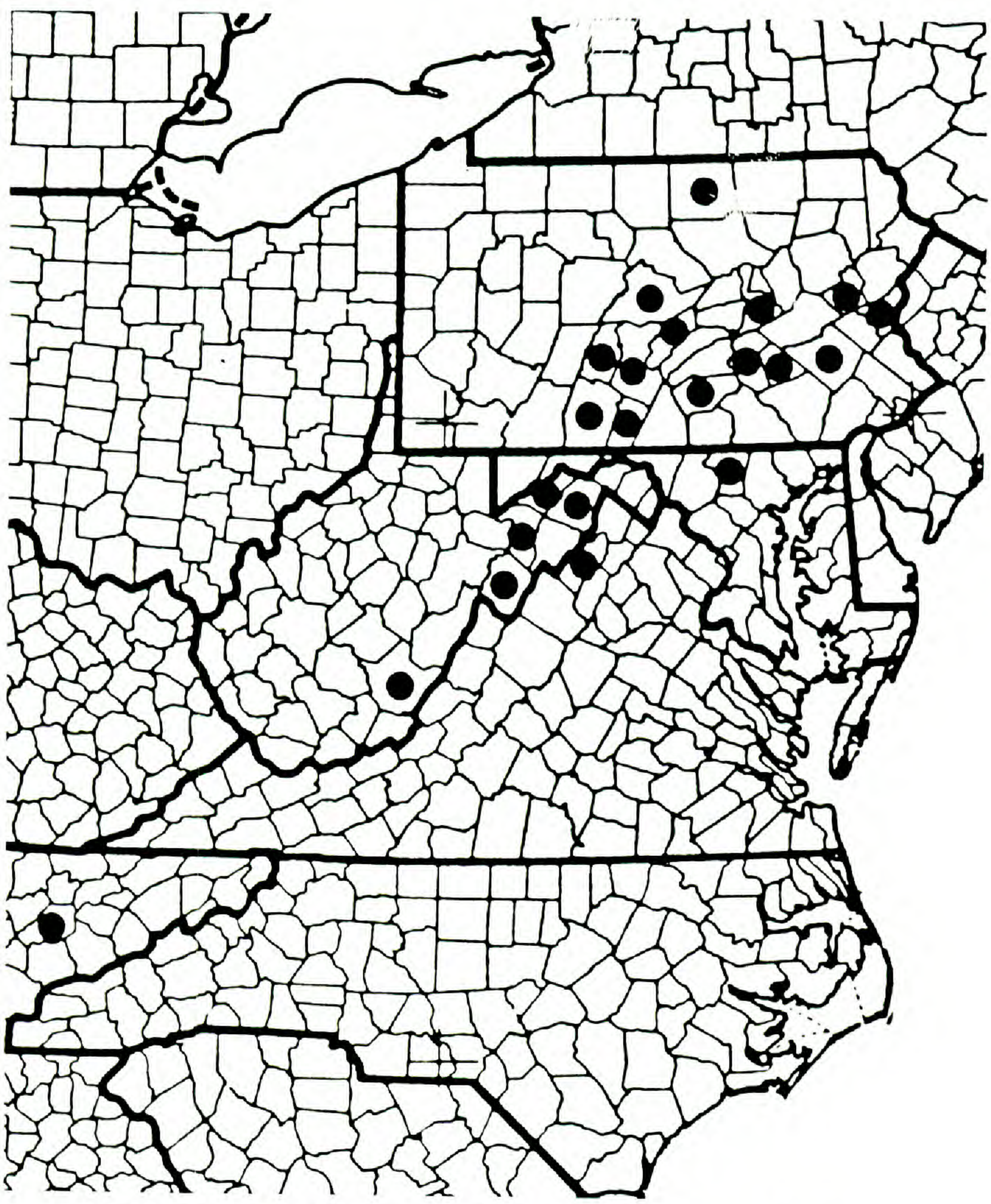

FIG. 5. Distribution by county of *Arabis laevigata* var. *burkii*.

these areas the stations are separated by 5 to 16 km. A specimen (GH) from limestone outcrops near Mascot, Knox County, Tennessee, was difficult to determine. Tentatively assigned to *A. laevigata* var. *burkii*, this presents an intriguing distributional question. That both taxa occur so sparingly in the sites occupied and that many sites, particularly in Virginia, are not occupied at all, poses some interesting biological questions as well.

ACKNOWLEDGMENTS

To my wife Ali I express great appreciation for her excellent illustration used as Figure 2. Thanks to Frosty Levy for reading and comments on an earlier draft. I also thank Rodney Bartgis for giving of his knowledge of West Virginia populations. Thanks to the following herbaria and their staff for loaning their collections: GH, NY, PAC, PH, US, and WVU. For the use of lab facilities I thank Dr. Khidir Hilu and for encouraging outside research, Dr. Duncan M. Porter, both of VPI.

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A TREATMENT OF *SCLERIA* (CYPERACEAE) FOR NORTH AMERICA NORTH OF MEXICO

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ABSTRACT

This treatment is based on field and herbarium research conducted over an eight year period and the examination of over 7,900 specimens of *Scleria* from the United States and Canada. Major emphasis is placed on achene sculpturing, and on pubescence of achenes, scales, bracts, leaves, and culms. Achenes from many species examined vary from glabrous to highly pubescent and from almost smooth to deeply papillose or reticulate. Scales, bracts, leaves, and culms on many species vary in vestiture. The taxonomic importance of these characters is questionable in view of the variability. Descriptions of ten species, a new combination, and a new key are presented. Several significant range extensions are reported.

The genus *Scleria* is found in all tropical maritime regions in the Old and New Worlds, inland in tropical forests and tropical mountains, and in most warm-temperate climates. It is best represented in the United States in the southeastern coastal regions, with some species extending north to Ontario and west to Minnesota and Texas. Core published the classical monographic study of *Scleria* of North and South America in 1936. Since his study, much research has been conducted on the genus, and a new monograph on the Western Hemisphere species is forthcoming. This paper presents a new taxonomic treatment for the species of the United States and Canada, including nomenclatural changes and significant range extensions.

This treatment is based on field and herbarium research conducted over an eight year period, which included examination of over 7,900 specimens. Several hundred specimens were collected, and vouchers will be deposited in SHST, SMU, TAES, and VDB. Measurements were taken from representative specimens for the species described. Descriptions are based on materials collected from the entire North American range of the species. Major emphasis is placed on achene sculpturing and on pubescence of achenes, scales, bracts, leaves, and culms. Achene surface sculpturing in some species varies from almost smooth to deeply papillose or reticulate, and vestiture varies from glabrous to highly pubescent. Scales, bracts, leaves, and culms on many species vary in vestiture. In view of this variability, the taxonomic importance of these characters is questionable. Many prior authors have attempted to use such variable characters to circum-

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scribe varieties in many North American *Scleria*, particularly in the Section *Tuberculatae*. In order to avoid the character overlap that results from such treatments, I have chosen to recognize species only.

TAXONOMY

SCLERIA Bergius in Kongl. Vetensk. Akad. Handl. 26:142, pls. 4, 5. 1765. TYPE SPECIES: *Scleria flagellum-nigorum* Bergius in Kongl. Vetensk. Akad. Handl. 26:142, pls. 4, 5. 1765.

Hypoporum Nees, Linnaea 9:303. 1834.
Cylindropus Nees, Linnaea 9:303. 1834.
Chondrolomia Nees in Mart., Fl. Bras. 2(1):173. 1842.
Hymenolytrum Nees in Mrt., Fl. Bras. 2(1):174. 1842.*Trachylomia* Nees in Mart., Fl. Bras. 2(1):174. 1842.
Mastigoscleria Nees in mart., Fl. Bras. 2(1):177. 1842.
Omoscleria Nees in Mart., Fl. Bras. 2(1):180. 1842.
Cryptopodium "Schrad. in Sched," Nees in Mart., Fl. Bras. 2(1):180. 1842.
Macrolomia Nees in Mart., Fl. Bras. 2(1):180. 1842.
Ophryoscleria Nees in Mart., Fl. Bras. 2(1):182. 1842.
Ophrydium Nees in Mart., Fl. Bras. 2(1):183. 1842.*Schizolepis* Nees in Mart., Fl. Bras. 2(1):186. 1842.
Diploscyphus Liebm., Kongel. Danske Vidensk. Selsk. Naturvidensk. Math. Afh. 2:262. 1850.

Tufted annuals or slender to robust rhizomatous perennials; culms sharply trigonous, angles often scabrous, leafy, sheaths overlapping, the lowest sheath bladeless; spikelets small, clustered in terminal or terminal and axillary fascicles; flowers monoecious, staminate and pistillate spikelets usually separated, occasionally born in the same clusters; pistillate spikelets 1-flowered, staminate spikelets many-flowered; perianth absent; stamens 1 – 3; style 2- or 3-cleft, basally slender to swollen, deciduous; achene supported on a hypogynium, or hypogynium absent; hypogynium, when present, usually adherent to the achene base and bearing 3 – 9 tubercles or a rough crust, or is extended into 3 prominent lobes; achene globose or ovoid to obovoid, crustaceous or bony, smooth or rough, usually whitish, sometimes gray or purplish.

Scleria is distinguished from other genera of Cyperaceae by its unisexual flowers and its white, bony achenes. A genus of about 200 species predominately native to topical and warm-temperature regions, very few ranging into cold-temperature latitudes. Named from the Greek *skleros* (hard), referring to the bone-like achenes.

KEY TO THE SPECIES

1. Achene body smooth or with longitudinal ridges (2)
1. Achene body rough, reticulate or with transverse ridges (7)

2. (1) Base of achene circular with a hypogynium (3)
2. Base of achene triangular without a hypogynium (4)
3. (2) Tubercles present between achene and hypogynium . . . . . 2. *S. oligantha*
3. Tubercles absent between achene body and hypogynium . . . . . 1. *S. triglomerata*
4. (2) Inflorescence a single terminal cluster (5)
4. Inflorescence of several axillary clusters (6)
5. (4) Base of achene triangular with a pair of iridescent pits on all sides .6. *S. georgiana*
5. Base of achene triangular without pits . . . . . 7. *S. baldwinii*
6. (4) Leaves, bracts and scales of inflorescence with long hairs . . . . . 8. *S. hirtella*
6. Leaves, bracts and scales of inflorescence glabrous . . . . . 9. *S. lithosperma*
7. (1) Achene body reticulate (8)
7. Achene body rough or transversely ridge, not reticulate (9)
8. (7) Base of achene without tubercles . . . . . 3. *S. reticularis*
8. Base of achene with 6 tubercles . . . . . 4. *S. ciliata* var. *curtissii*
9. (7) Base of achene triangular without a hypogynium . . . . . 10. *S. verticillata*
9. Base of achene obscurely triangular with a hypogynium (10)
10. (9) Achene 2 – 3 mm long . . . . . 4. *S. ciliata* var. *ciliata*
10. Achene 1 – 2 mm long . . . . . 5. *S. pauciflora*

1. SCLERIA TRIGLOMERATA Michx., Fl. Bor. Amer. 2:168. 1803. Fig. 1.

Perennial; rhizomes 3 – 5 mm thick, woody, nodulose, usually clustered; culms erect, 10 – 100 cm tall, usually clustered, 2 – 6 mm thick basally; sharply trigonous, glabrous or nearly so, somewhat roughened distally; sheaths purple, scarcely winged, lower ones bladeless; ligule truncate to ovate, rigid, pubescent or glabrous; blades 15 – 30 cm long, 3 – 9 mm wide, rigid, scabrous on the margins and keel, sometimes slightly pubescent, shorter than to as long as the culms, a short taper to the apex; lower bract 2 – 10 cm long, appearing as a continuation of the culm; inflorescence terminal and axillary, each cluster with 3 – 12 spikelets, 5 – 6 mm long, the lateral ones on erect peduncles, spikelets few-flowered; staminate spikelets 5 – 6 mm long, with 2 or 3 flowers each; pistillate scales castaneous to purplish-tinged, the midrib excurrent, ovate-orbicular; staminate scales castaneous to brownish, lanceolate, acuminate; hypogynium obscurely trigonous, covered with a white papillose crust, tubercles absent; achene 1.5 – 3 mm long, ovoid to globose, smooth, shiny, bright white, obtuse. Moist sandy soil, in meadows, thickets, pine and hardwood forests, and banks of streams and lakes. Flowers from June-September.

Distribution: Massachusetts west to Ontario and Iowa, south to Texas, east to Florida; Puerto Rico; Mexico.

Remarks: *Scleria triglomerata* is the most common North American *Scleria*. Core (1936) and Godfrey and Wooten (1979) treated *S. minor* (Britton) Stone as synonymous with *S. triglomerata*. Core (1966), Fairey

(1967), Correll and Johnston (1970), and Correll and Correll (1975) treated *S. minor* as a distinct species. Numerous specimens of *S. triglomerata* and *S. minor* examined in this study were previously determined by Core, Fairey, and Johnston. I agree with Core (pers. comm.) that a series of variations occurs between *S. triglomerata* and *S. minor*. Based on observations made during this study, *S. minor* is treated as a variation of *S. triglomerata*.

Fernald (1936) and others have separated *S. triglomerata* into *S. flaccida* Steud. and *S. nitida* Willd. These taxa represent variations of *S. triglomerata*, and their classification as separate species can not be justified. *Scleria triglomerata* closely resembles *S. oligantha* Michx., and the two are frequently difficult to distinguish. In many cases, correct identification is possible only after an examination of the achenes. Achenes of *S. triglomerata* are non-tuberculate, while those of *S. oligantha* have 8 or 9 small hemispheric white tubercles beneath the achene.

2. SCLERIA OLIGANTHA Michx., Fl. Bor. Amer. 2:167. 1803. Fig. 1. TYPE: U.S.A.: CAROLINA. In pratensibus sylvaticus Carolinae (HOLOTYPE: P!; holotype photo: GH!).

Perennial; rhizomes 2–5 mm thick, nodulose, relatively soft; culms erect, 30–70 cm tall, 2–3 mm thick, sharply trigonous, glabrous or nearly so; sheaths pubescent or glabrous, narrowly winged, the lower ones purplish-tinged; ligule 0.5–1.5 mm long, ovate, scarious margined, pubescent; blades 12–15 cm long, 2–6 mm wide, glabrous except for the scabrous to hispid margins and midribs beneath, somewhat revolute when dry; bracts ciliate, pubescent on adaxial side, the longest one appearing as a continuation of the culm; inflorescence of 2–5 dense clusters, terminal and on flexuous axillary filiform peduncles, peduncle angles scabrous; scales lanceolate-ovate, purplish-tinged, mucronate; hypogynium a narrow obtusely triangular border, with 8 or 9 small hemispheric white tubercles beneath the achene; achene 2.5–4 mm long, ovoid, white, smooth, shiny, shorter than the scales, apically pointed. Moist or occasionally dry sandy soil in pinelands, seldom in meadows or open areas. Flowers from April-August.

Distribution: New Jersey west to Missouri, south to Texas, east to Florida; Puerto Rico; Mexico; Guatemala; Honduras.

Remarks: *Scleria oligantha* closely resembles *S. triglomerata* Michx., and the two are frequently difficult to distinguish except by an examination of their achenes. Achenes of *S. oligantha* have 8 or 9 small hemispheric white tubercles beneath the achene, while those of *S . triglomerata* are non-tuberculate, with a white papillose crust beneath the achene.

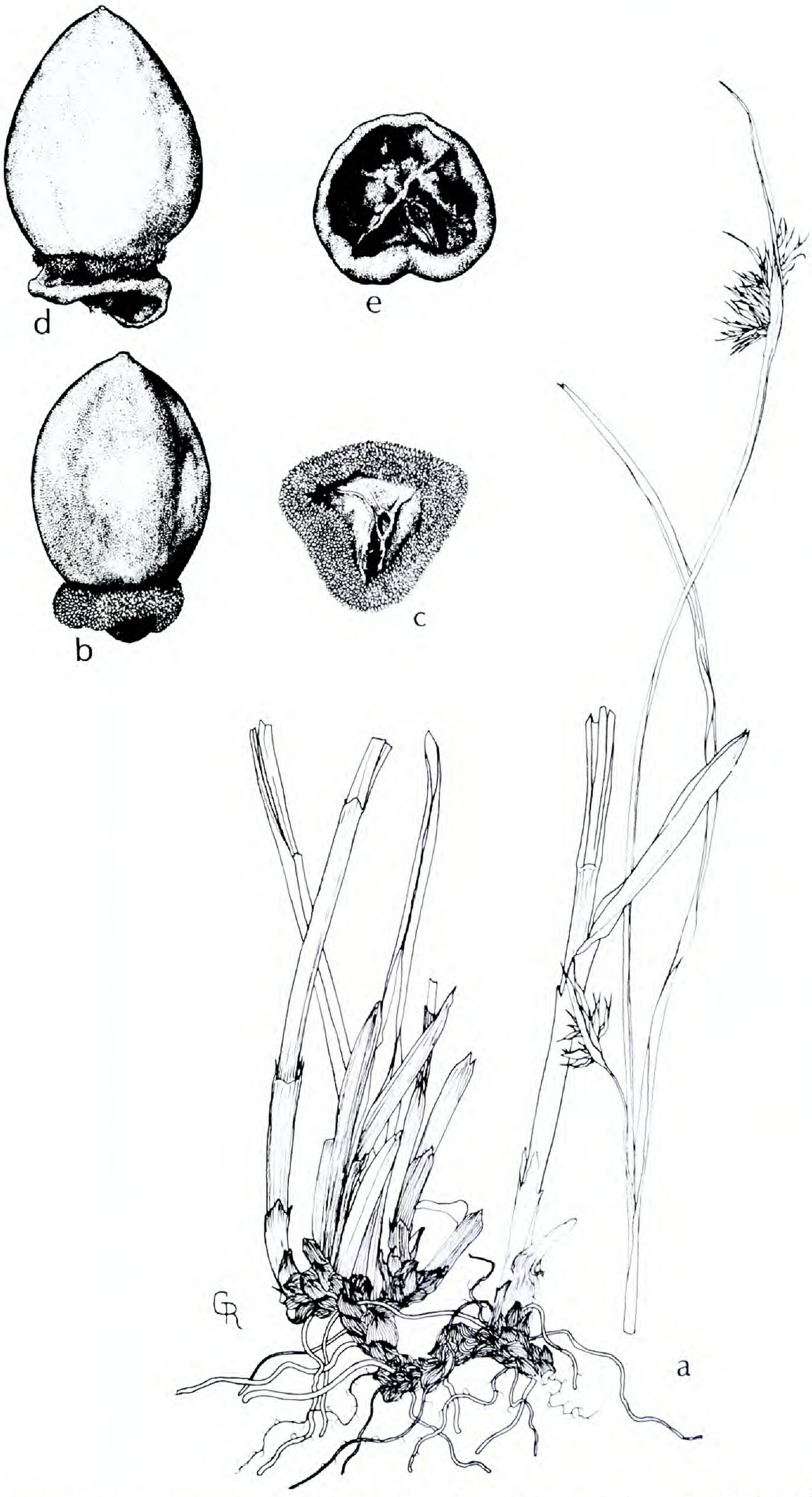

FIG. 1. a – c, *Scleria triglomerata*: a, habit; b, achene, lateral view; c, achene, basal view; d – e, *Scleria oligantha*: d, achene, lateral view; e, achene, basal view. (From: Godfrey and Wooten 1979, with permission.)

3. Scleria reticularis Michx., Fl. Bor. Amer. 2:167. 1803. Fig. 2.
Type: U.S.A.: Carolina. Hab. in Carolina (isotype: P!).

Perennial with short rhizomes 1 – 2 mm thick, or annual with fibrous roots; culms clustered or solitary, triangular, or obscurely so, glabrous to slightly pubescent, 20 – 80 cm tall, erect to reclining, 1 – 3 cm thick; sheaths purplish to castaneous, narrowly to broadly 3-winged, the wings smooth to scabrous; ligule short, obtuse to acuminate; blades 10 – 30 cm long, 1 – 4 mm wide, flat, thin, shorter than the culm, glabrous to slightly pubescent, sometimes scabrous on the margins; bracts 1 – 3 mm wide, glabrous to slightly pubescent; inflorescence a terminal and axillary panicle, sessile or on peduncles 1 – 50 mm long, few-flowered; staminate spikelets lanceolate, stramineous; pistillate scales ovate-lanceolate, acuminate, stramineous; hypogynium 3-lobed, lobes lanceolate, obtuse, appressed to the base of the achene; achene 1 – 2.5 mm long, obscurely to deeply reticulate, glabrous to pubescent, globose-elliptic, dull to bright white, sometimes gray or purplish. Open sandy areas, often in shallow water in ponds, bogs, meadows, wet pinelands, depressions and savannas. Flowers from June-November.

Distribution: Massachusetts west to Wisconsin, south to Texas, east to Florida; Bahama Islands; Cuba; Jamaica; West Indies; Puerto Rico; Haiti; Mexico; Belize; Guatemala; Honduras; El Salvador; Nicaragua; Costa Rica; Panama; Trinidad; Colombia; Bolivia; Brazil.

Remarks: *Scleria reticularis* is one of the most common and variable of the North American *Scleria*. Its variability, especially in achene sculpturing and vestiture, has caused much taxonomic difference of opinion. Core (1936) separated *S. setacea* Poir. from *S. reticularis* based on pilose ridges on the achene, while those of his *S. reticularis* had glabrous achenes. Fernald (1943) resolved the problem of nomenclature concerning *S. setacea* and changed the name to *S. muhlenbergii* Steud. This change was followed by Steyermark (1963) and Core (1966). Radford, et al. (1968) treated *S. setacea*, *S. muhlenbergii*, and *S. reticularis* var. *pubescens* Britton synonymously with *S. reticularis*.

Fairey (1967) discussed the integradation and variation, especially in the achenes. He found that achenes vary from glabrous to heavily pubescent. Based on these observations, Fairey reclassified *S. muhlenbergii* as *S. reticularis* var. *pubescens*. Achenes also vary in sculpturing from those having deep reticulations covering the surface of the achene to those with a smooth surface. Fairey (1975) determined that *S. stevensiana* Britton represents a robust form of *S. reticularis*, and that *S. anceps* Liebm. represents a form with narrowed, pointed achenes and dark scales.

FIG. 2. a – b, *Scleria reticularis*: a, habit; b, achene, lateral and basal views; c – e, *Scleria ciliata*: three achenes, lateral and basal views, to show variation. (From: Godfrey and Wooten 1979, with permission.)

The designation of the different varieties has been based primarily on achene sculpturing and vestiture. It is often difficult to determine where one variety ends and another begins; therefore, distinct varieties are not recognized in this treatment.

4a. SCLERIA CILIATA Michx., Fl. Bor. Amer. 2:167. 1803. Fig. 2. TYPE: U.S.A.: CAROLINA. Carolinae poir M. Michaux (ISOTYPE:P!).

Perennial; rhizomes 1 – 5 mm thick, nodose, becoming intricately layered in older plants; culms erect, 20 – 70 cm tall, 1 – 3(– 4) mm thick, from almost glabrous to more commonly pubescent, sharply triangular; sheaths brownish with some purple near the distal end, usually pubescent, the lower ones bladeless; ligule 1 – 5 mm long, subrotund to rotund; blades (1 –)10 – 45 cm long, 1 – 6 mm wide, keeled, glabrous to pubescent on both abaxial and adaxial sides, shorter than to much longer than the culm; bracts 2 – 5, shorter than to much longer than the inflorescence, glabrous to ciliate; inflorescence terminal and axillary, spikelets 3 or more, clustered, sometimes arising on short peduncles from the lower axils; staminate spikelets 3 – 4 flowered; pistillate scales 4 – 6 mm long, ovate, acuminate; keel glabrous to ciliate, greenish in young plants, becoming purple at maturity; hypogynium narrow, obtusely trigonous, with 3 entire or 2-lobed tubercles; achene 2 – 3 mm long, white, sometimes gray or purplish, globose, usually mucronate-apiculate, transversely verrucose-papillate, sometimes obscurely so or smooth. Moist or dry sandy soil. Flowers from April-November.

Distribution: Virginia west to Missouri, south to Texas, east to Florida; Cuba; West Indies; Puerto Rico; Dominican Republic; Mexico; Belize; Honduras.

Remarks: Over five hundred specimens of *S. ciliata* were examined in this study. Variation was observed in the size, sculpturing, and tuberculation of the achenes. Achene length varied from (1.5 –)2.0 – 3.0 mm. Achene surface sculpturing varied from deeply verrucose-papillate to almost smooth. Tubercle size and numbers also varied from three relatively large, distinct tubercles per achene to three deeply 2-lobed tubercles to six smaller distinct tubercles. These characteristics intergrade with those of *S. pauciflora* (see *S. pauciflora*). These taxa are closely related and may be varieties of one polymorphic species.

4b. SCLERIA CILIATA Michx. var. **curtissii** (Britton) Kessler, comb. nov. *Scleria curtissii* Britton in Small, Fl. SE U.S. 200. 1903. TYPE: U.S.A.: FLORIDA. Duval Co.: In pinelands near Jacksonville, 1894, *Curtiss 4793* (HOLOTYPE: NY!).

Same as the species except achenes about 2 mm long, white, globose,

irregularly ridged-reticulate, apiculate. Rare in moist sandy soil near the edge of pinelands. Flowers from June-November.

Distribution: Southern Florida north along the Atlantic Coastal Plain to South Carolina; Cuba.

Remarks: *Scleria ciliata* var. *curtissii* has been recognized by Small (1903, 1933), Core (1936), Fairey (1967), and Long and Lakela (1971) as *Scleria curtissii*. Fairey reported that *S. curtissii* closely resembles *S. pauciflora* morphologically, but distinguished it from that species by its reticulate achenes. Fairey (1969) combined *S. curtissii* with *S. pauciflora* based on "general habit." He also noted that the achenes of *S. curtissii* indicate a closer relationship with *S. ciliata* than with *S. pauciflora*. *Scleria ciliata* var. *curtissii* has been rarely collected, with only four specimens cited by Fairey. Twenty-six specimens were examined in this study. Based on scanning electron microscopy (SEM) studies of the micromorphology of achenes, scales, leaves, and culms, *S. curtissii* more closely resembles *S. ciliata* than *S. pauciflora*. Therefore, in this study, *S. curtissii* is treated as a variety of *S. ciliata*.

Eight hundred specimnes of *S. ciliata* and *S. pauciflora* were examined in this study. Achene surface sculpturing on both species varied from almost smooth to deeply verrucose-papillate. Achenes from many of the specimens were lightly reticulate. Tubercle size and numbers also varied in both *S. ciliata* and *S. pauciflora*. Based on these observations and those of Robinson (1964) working with *S. hirtella* complex (see *S. hirtella* and *S. pauciflora*), evidence indicates that *S. pauciflora* may be a variety of *S. ciliata*. These taxa need additional study to justify a combination; therefore, in this study the two taxa are treated as distinct species.

5. SCLERIA PAUCIFLORA Muhl. in Willd., Sp. Pl. 4:318. 1806. TYPE: U.S.A.: CAROLINA. Habitat in pratensibus sylvaticus Carolinae (ISOTYPE: NY!).

Perennial; rhizomes 3–5 mm thick, nodulose, elongate, hard, clustered; culms erect, 20–50 cm tall, 2–3 mm thick, triangular, margins usually scabrous, glabrous to slightly pubescent, sheaths purplish-brown, basally puberulent, apically ciliate or glabrate, the lower ones bladeless; ligule short, obtuse, scabrous, often folded and/or pleated, shorter than the culm; bracts erect, longer than the inflorescence, the longest one appearing as a continuation of the culm, margins glabrous or scaberulate; inflorescence terminal and axillary, spikelets 3- to 6-flowered, clustered, sometimes arising on long filiform peduncles from the lower axils; pistillate scales ovate-lanceolate, acuminate, purplish-tinged, midrib ciliate; hypogynium narrow, obtusely trigonous, with 6 globose tubercles; achene 1–2 mm long, white, sometimes gray or purplish,

oblong to globose, apiculate, irregularly transversely verrucose-papillate. Moist sandy soil in meadows or lightly wooded areas. Flowers from June-October.

Distribution: New Hampshire west to Kansas, south to Texas, east to Florida; Cuba; Mexico; Belize.

Remarks: *Scleria pauciflora* closely resembles *S. ciliata* morphologically. The two species are usually distinguished on the basis of achene size and number of tubercles. Fairey (1967) described the achenes of *S. ciliata* as being 2 – 3 mm long and bearing three tubercles, and those of *S. pauciflora* as being 1 – 2.5 mm long and bearing six tubercles. Five hundred specimens of *S. ciliata* and 300 specimens of *S. pauciflora* were examined in this study. Achene size and tuberculation varied in both species with much overlapping of characteristics being observed. Achene tuberculation varies in *S. ciliata* from three relatively large distinct tubercles per achene to three deeply 2-lobed tubercles to six smaller distinct tubercles, while achenes of *S. pauciflora* have six distinct tubercles. Achene size in *S. ciliata* varies from 1.5 – 3.0 mm, while achenes of *S. pauciflora* vary from 1 – 2.5 mm. The intergradation of achene size and tuberculation make it difficult, if not impossible, to determine some specimens based solely on an examination of achenes. Scales, pubescence, culm length, and culm diameter also intergrade between the two taxa. These observations correlate with those of Robinson (1964) on the polymorphic species *S. hirtella*, and indicate that *S. pauciflora* may be a variety of *S. ciliata*. Since *S. pauciflora* so closely resembles *S. ciliata* it is not illustrated. These taxa need additional study to justify a combination; therefore, the two taxa are treated as distinct species.

6. SCLERIA GEORGIANA Core, Brittonia 1:243. 1943. Fig. 3. *Scleria gracilis* Ell., Sketch Bot. S. Carolina 2:557. 1824. TYPE: U.S.A.: GEORGIA. Camden Co.: near St. Mary's, [1812?], *Baldwin s.n.* (HOLOTYPE: NY!). Non L.C. Rich. Act. Soc. Hist. Nat. Paris 1:113. 1792.

Perennial; rhizomes 2.5 – 5 mm thick, nodose, becoming densely compacted in older plants; culms erect, 30 – 50 cm tall, 1 – 2 mm thick, wiry, trigonous, glabrous; sheaths purplish, often truncate, glabrous, the lower ones bladeless; blades 12 – 16 cm long or longer, 1 – 2 mm wide, few, glabrous, linear or filiform, involute, shorter than the culm; lower bract 1 – 8 cm long, 1 – 2 mm wide, appearing as a continuation of the culm; inflorescence a single terminal fascicle of 2 – 5 ovate spikelets, 3 – 5 mm long; staminate scales lanceolate, acuminate, reddish-brown; pistillate scales ovate-lanceolate, acuminate, reddish-brown; hypogynium absent; achene shorter than the scales, about 2 mm long, ovoid, white, sometimes purplish, smooth or longitudinally ridged, basally trigonous,

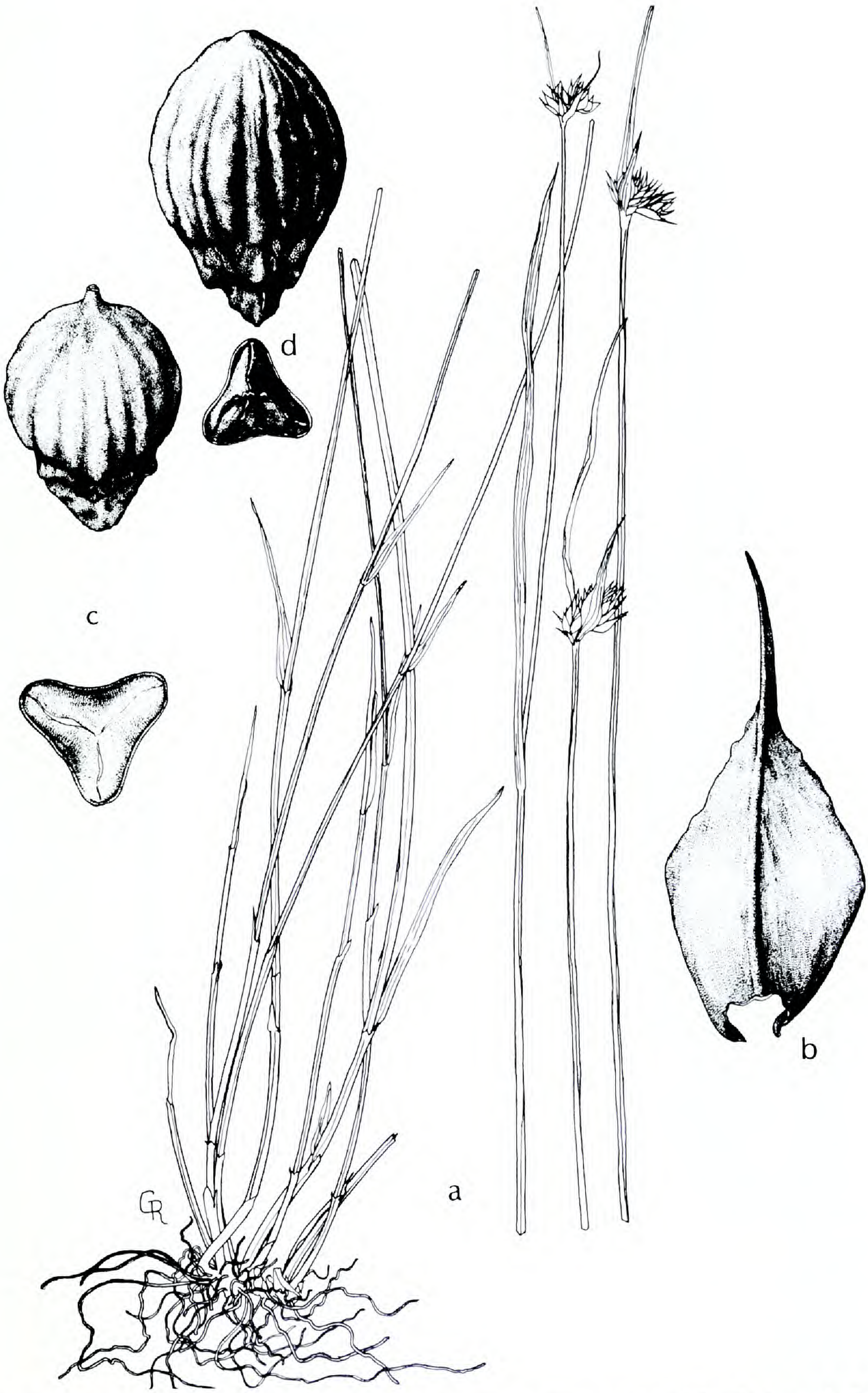

FIG. 3. a—c, *Scleria baldwinii*: a, habit; b, scale; c, achene, lateral and basal views; d, *Scleria georgiana*: achene, lateral and basal views. (From: Godfrey and Wooten 1979, with permission.)

concave on the sides, each depression containing 2 iridescent pits. Rare in moist loam. Flowers from April-September.

Distribution: North Carolina south to Florida, west to Texas; Cuba; Jamaica; Dominican Republic; Belize; Brazil.

Remarks: *Scleria georgiana* resembles *S. baldwinii*, and the two are frequently difficult to distinguish except by achene characteristics. Achenes of *S. georgiana* are about 2 mm long, basally trigonous, concave on the sides, each depression containing 2 pits, while those of *S. baldwinii* are 3 – 4 mm long and contain no pits at the achene base.

7. SCLERIA BALDWINII (Torr.) Steud., Syn. Pl. Cyp. 175. 1855. Fig. 3.
Hypoporum baldwinii Torr., Ann. Lyceum Nat. Hist. New York. 3:382. 1836. TYPE: U.S.A.: GEORGIA. [1811 – 1812], *Baldwin s.n.* (HOLOTYPE: NY, microfiche SMU!; ISOTYPE: GH!).

Perennial; rhizomes 3 – 7 mm thick, hard, nodose, clustered; culms erect, frequently caespitose, 30 – 90 cm tall, sharply triangular, slightly canaliculate, angles smooth to slightly scabrous above; sheaths reddish-brown basally, glabrous to slightly scabrous, the lower ones bladeless; blades (1 –)10 – 50 cm long, 1 – 5 mm wide, linear, rigid, keeled, margins glabrous to slightly scabrous; bracts ovate, glabrous to slightly scabrous, often purplish-tinged, 1 – 4 mm wide, linear, lowest bract 4 – 15 cm long; inflorescence a single capitate cluster 1 – 2 cm long; staminate scales membranous, purplish to stramineous, glabrous to puberulent; pistillate scales rigid, ovate, acuminate, purplish to stramineous; hypogynium a small brownish ridge just above the pointed base or absent; achene 3 – 4 mm long, ovoid, white, sometimes gray or purplish, smooth or longitudinally ribbed, obscurely trigonous, apiculate, base triangular, pointed concave on the sides, without pits in the depressions. Uncommon in wet pinelands and savannas, hammocks, borders of lagoons, ponds, and depressions along the Atlantic and Gulf of Mexico coastal plains. Flowers from May-October.

Distribution: SC s to Fl, w to TX; Cuba.

Remarks: *Scleria baldwinii* resembles *S. georgiana*, but can be distinguished by an examination of the achenes (see *S. georgiana*). Many specimens of *S. baldwinii* examined during this study were incorrectly identified as *S. triglomerata*. *S. baldwinii* is a more robust species than *S. triglomerata* and can be distinguished by an examination of the achenes. Achenes of *S. baldwinii* are 3 – 4 mm long with a pointed, triangular base, while those of *S. triglomerata* are 1.5 – 3.0 mm long with an obscurely trigonous, white, papillose crust at the base of the achene.

8. SCLERIA HIRTELLA Sw., Prodr. Veg. Ind. Occ. 19. 1788. Fig. 4. TYPE: JAMAICA: *Swartz s.n.* (HOLOTYPE: BM!; ISOTYPES: B, M, P!, S).

Perennial; rhizomes 2–4 mm thick, elongate, sometimes clustered, aromatic; culms erect, 15–65 cm tall, 2–4 mm thick, acutely triangular, apex glabrous to pubescent; sheaths greenish, sometimes stramineous, pubescent; ligule minute or absent; blades 4–20 mm wide, linear, flat to involute, pubescent to nearly glabrous; bracts attenuate, long-pilose; inflorescence a terminal glomerule and an interrupted spike of 3–9 sessile glomerules, often nodding; rachis pubescent; staminate scales obtuse, narrow, brownish; hypogynium a small brownish ridge at the base of the achene or absent; achene 1–2 mm long, white to gray, usually shiny, smooth to lightly or deeply papillose, mucronate, obscurely trigonous, obovoid to subglobose, base cuneate-attenuate with 9–12 irregular minute pits. Wet pinelands and savannas. Flowers from May-November.

Distribution: Along the Atlantic and Gulf of Mexico coastal plains from Georgia south to Florida, east to Texas; Cuba; Jamaica; Puerto Rico; Haiti; Dominican Republic; Lesser Antilles; Guadaloupe; Mexico; Belize; Guatemala; Honduras; Nicaragua; Costa Rica; Panama; French Guiana; Brazil; Argentina; Chile; Galapagos Islands; Africa; Madagascar.

Remarks: Robinson (1964, 1966), based on achene morphology, combined *S. interrupta* Rich., *S. distans* Poir., *S. lindleyana* Clarke, *S. tricholepis* Nelms, *S. melanotricha* var. *glabrior* Clarke, and *S. tenuiflora* Willd. as synonyms under the polymorphic *S. hirtella*. Fairey (1967), also working with a basis of achene morphology, combined *S. pinetorum* Britton, *S. motemboensis* Britton, and *S. doradoensis* Britton with *S. hirtella*. Raynal (1976) examined some of the types and other specimens of *S. hirtella, S. interrupta, S. distans, S. lindleyana*, and *S. tricholepis* previously examined by Robinson. Based primarily on achene sculpturing, Raynal treated *S. hirtella, S. interrupta*, and *S. distans* as distinct species. He combined *S. lindleyana* with *S. hirtella*, and *S. melanotricha* var. *glabrior, S. tricholepis*, and *S. tenuiflora* with *S. interrupta*. Core (1936), placing too much emphasis on "geographical remoteness" without recognizing that adequate collections had not yet been made, treated all of the above New World taxa as distinct species.

Neither Swartz's first account of *S. hirtella* in his Prodromus of 1788 nor the more detailed description in his Flora of 1797 contained any information on surface features of the achenes. Robinson observed that the type at Munich has a very lightly papillose surface, while the type at the British Museum appears, to the unaided eye, to be almost smooth, but some superficial irregularities can be observed under 40X magnification.

Research in this study shows that the apex on dried immature achenes

frequently appears to have a smooth surface, while the basal portion of the same achene may be papillose or sometimes reticulate. Some mature specimens were observed which contain both smooth and slightly papillose achenes on the same specimen.

This treatment follows those of Robinson and Fairey and considers *S. hirtella* to be highly variable in achene sculpturing. This variability accounts for its long synonymy. *Scleria hirtella* and *S. lithosperma* are the only two species of North American *Scleria* found in both the New and Old Worlds.

9. Scleria lithosperma (L.) Sw., Prodr. Veg. Ind. Occ. 18. 1788. Fig. 4. *Scirpus lithospermus* L., Sp. Pl. 51. 1753. Type: INDIA. (LINN?).

Perennial; rhizomes 2 – 4 mm thick, short, nodulose; culms ascending to erect, 30 – 60 cm tall, filiform to 2 mm thick, triangular, often caespitose, glabrous to slightly pubescent; sheaths thinly pilose to glabrous; the lower ones purplish and bladeless; ligule short, rigid, triangular, pilose; blades 10 – 20 cm long, 1 – 3 mm wide, reclining, involute, keeled, glabrous, margins and keel scabrous; bracts filiform, glabrous; the inflorescence usually subtended by a leaf-like bract; inflorescence a terminal sessile spikelet and 1 – 4 interrupted axillary spikelets on short peduncles; spikelets 1- to 3-flowered; pistillate and staminate scales dark brown, ovate-lanceolate, pistillate ones exceeding the achene; hypogynium a brownish band above the achene base or obsolete; achene 2 – 2.5 mm long, white or grayish, smooth to slightly reticulate or muricate, shiny, oblong to ovate-elliptic, umbonate, base triangular, attenuate, non-porose. Pinelands, moist to dry open woods, hammocks, and shallow soil near limestone. Flowers from April-November.

Distribution: Florida west to Louisiana; Bahama Islands; Cuba; Jamaica; British West Indies; Dominica; Puerto Rico; Dominican Republic; Haiti; Mexico; Belize; Guatemala; Nicaragua; Costa Rica; Caicos Islands; Fiji; Philippine Islands; Africa; Asia; Malaysia; Australia; all tropical and maritime regions in the Old and New Worlds.

Remarks: Govindarajalu (1970) describes two new varieties of *S. lithosperma*, var. *multispiculata* and var. *muricata*, from south India. Variety *muricata* is distinguished by the presence of muricate achenes. In the present study specimens from the West Indies and Central America had muriculate achenes. These specimens match specimens determined by Govindarajalu to be var. *muricata* (P!), and thus extend the range of this variety to the New World.

Scleria lithosperma is the most widely distributed species of *Scleria*. *Scleria lithosperma* and *S. hirtella* are the only two species of North American *Scleria* found in both the New and Old Worlds.

FIG. 4. a – b, *Scleria verticillata*: a, habit; b, achene, lateral and basal views; c, *Scleria hirtella*: achene, lateral and basal views; d – e, *Scleria lithosperma*: d, inflorescence branch or tip; e, achene, lateral and basal views. (From: Godfrey and Wooten 1979, with permission.)

10. Scleria verticillata Muhl. ex Willd., Sp. Pl. 4:317, excl. syn Michx. 1805. Fig. 4. Type: U.S.A.: Pennsylvania. in Herb. Willd. 17326, *Muhlenberg s.n.* (holotype: B).

Annual with aromatic capillary fibrous roots; culms ascending to erect, 10 – 60 cm tall, filiform to slender, trigonous, glabrous to pubescent, sheaths usually pilose; ligule minute, truncate, hirsute, or absent; blades 3 – 30 cm long, shorter than the culm, 0.5 – 3.0 mm wide, glabrous to pubescent, flat, nodding to ascending; bracts 6 – 7 mm long, glabrous, often caudate; inflorescence a terminal sessile glomerule and 1 – 7 interrupted axillary sessile glomerules; scales glabrous, oblong-lanceolate, stramineous to castaneous with a prominent green keel; hypogynium a brownish band near the achene base, or absent; achene 1 – 1.5 mm long, white, sometimes purplish, reticulate to verrucose, mucronate, globose to trigonous, the base triangular, constricted to an almost attenuate stalk with 4 – 5 pores on each side. Wet sandy soil and moist pinelands along the Atlantic and Gulf of Mexico coastal plains, inland on banks of major rivers, and along the banks of the Great Lakes. Flowers from June-October.

Distribution: Ontario west to Minnesota, south to Texas, east to Florida; Bahama Islands; Cuba; Jamaica; Puerto Rico; Mexico; Belize; Honduras; Nicaragua; Costa Rica; Panama; Colombia; Dutch Guiana; Brazil.

Remarks: *Scleria verticillata* resembles *S. hirtella* morphologically, and the two are frequently difficult to distinguish. *Scleria verticillata*, an annual, is best distinguished by its glabrous scales; those of the perennial *S. hirtella* are pilose.

Fairey (1975) separated *S. tenella* Kunth from *S. verticillata* without stating his reasons and combined *S. areolata* Lundell, *S. liebmanni* Steud., and *S. micrococca* (Liebm.) Steud. with *S. tenella*. Core (1936) combined *S. tenella* with *S. verticillata* and *S. liebmanni* with *S. micrococca*. During the present study, many specimens determined as *S. tenella* by Fairey were examined. No significant differences between these specimens and over 400 specimens of *S. verticillata* could be found. Based on these observations and those of Robinson (1964), I combine all of the above taxa with *S. verticillata*.

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DOCUMENTED PLANT CHROMOSOME NUMBERS 1987: 1. MISCELLANEOUS COUNTS FROM WESTERN NORTH AMERICA

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Chromosome numbers were determined for 183 individuals representing 93 taxa in 53 genera from western North America. The need for documentation of such reports as aids in reconstructing biogeographic histories, in determining the evolution of infraspecific polyploidy and in the determination of the amount and nature of chromosome diversity within a taxon have been stated many times (Mosquin and Hayley 1966; Strother 1972; Semple et al. 1983).

MATERIALS AND METHODS

Mitotic chromosome counts were made from root-tips that were treated with 0.05% colchicine for two hours, fixed in a mixture of ethanol and glacial acetic acid (3:1), subsequently hydrolyzed in 1N HCl at 60° C for 10-12 minutes, and then squashed in 2% acetic orcein stain. Meiotic counts were made from flower-buds that were fixed in absolute ethanol - chloroform - glacial acetic acid (3:4:1). Anthers were squashed with 1% acetic orcein stain. Slides were made permanent with the dry ice method. Specimens prefixed by UAC were collected by CCC and associates during an expedition to the Brooks Peninsula refugium arranged by the British Columbia Provincial Museum. For some taxa only the rootstocks or flower-buds were returned to the laboratory for chromosome number determinations, thus vouchers are not available. All other specimens were collected by CCC. Voucher specimens were deposited in the Herbarium of the Department of Biological Sciences, University of Calgary (UAC).

RESULTS

APIACEAE

LIGUSTICUM CALDERI Mathias & Constance. $2n = 66$ CANADA. BRITISH COLUMBIA. Brooks Peninsula, Gentiana Lake, *UAC39634*.

ASTERACEAE

APARGIDIUM BOREALE (Bong.) Torr. & Gray. $2n = 18$ CANADA. BRITISH COLUMBIA. Brooks Peninsula, Gentiana Lake, *UAC50027*.

SIDA 12(2):409–417. 1987.

ARNICA CHAMISSONIS Less. $2n = 57$ CANADA. BRITISH COLUMBIA. Kelowna, *1063*.

A. LATIFOLIA Bong. $2n = 38$. CANADA. BRITISH COLUMBIA. Brooks Peninsula, Doom Mountain, *no voucher*.

ARTEMISIA TRIFURCATA Stephan. ex Sprengel. $2n = 18$. CANADA. BRITISH COLUMBIA. Brooks Peninsula, Doom Mountain, *no voucher*.

ASTER ALPINUS L. $2n = 18$. CANADA. ALBERTA. Calgary, *647*; Longview *656*; Kananaskis Lake, *382, 383; Redwood Meadows, 649*.

A. (VIRGULUS) ERICOIDES L. ssp. PANSUS (Blake) A. G. Jones. $2n = 10$. CANADA. BRITISH COLUMBIA. Kamloops, *853*. $2n = 10 + 3b$. CANADA. ALBERTA. Edworthy Park, *449*.

A. FOLIACEUS Lindley. $2n = 64$. CANADA. BRITISH COLUMBIA. Brooks Peninsula, Cape Cook Lagoon, *no voucher*.

A. INTEGRIFOLIUS Nutt. $2n = 18$. CANADA. ALBERTA. N of Livingston Falls, 1107.

A. MODESTUS Lindley. $2n = 18$. CANADA. ALBERTA. 30 km S of Livingston Falls, *1115*.

A. SIBIRICUS L. $2n = 18$. CANADA. NORTHWEST TERRITORIES. Hwy 3, 67 km N of Chan Lake, S of Edzo, *2212*; Hwy 3, 24 km N of Chan Lake, *2218*; Dempster Hwy, 1 km N of Arctic Red River, *2631*. YUKON. Campbell Hwy, Bruce Lake overlooking Ross River, *2276*; Dawson, Bonanza Rd. along Bonanza Creek, *2476*; White River, 2 km SE of White River Bridge, *2484*; Dempster Hwy, *2587*; 32 km S of Engineer Creek Campground, *2636*; 8 km S of Pelly Crossing, *2664*. UNITED STATES. ALASKA. Steese Hwy, 2 km NE of Captain Creek, *2397*; 1 km SW of bridge over Birch Creek, *2439*; ALASKA Hwy, 2 km W of Shaw Creek, *2444*; Glenn Hwy, 38 km NE of Nebesna junction, *2549*; Glenn Hwy, 8 km SW of Indian River, *2556*.

A. SUBSPICATUS Nees. $2n = 48$. CANADA. BRITISH COLUMBIA. 31 km W of Salmon Arm, *1120*. $2n = 90$. BRITISH COLUMBIA. Brooks Peninsula, Gentiana Lake, *UAC39640*.

CHAENACTIS DOUGLASII (Hook.) Hook. & Arn. $2n =$ ca 26. CANADA. BRITISH COLUMBIA. Kamloops, *616*.

CREPIS TECTORUM L. $2n = 8$. CANADA. ALBERTA. Edmonton, *498*.

ERIGERON ACRIS L. var. ASTEROIDES (Andrz.) DC. $2n = 18$. CANADA. ALBERTA. Plateau Mountain, *218*. BRITISH COLUMBIA. W of Manning Provincial Park, *302*; W of Glacier National Park, 6.3 mi W of Columbia River, *352*.

E. ACRIS L. var. DEBILIS A. Gray. $2n = 18$. CANADA. ALBERTA. Plateau Mountain, *377*; Redwood Meadows, *441*. NORTHWEST TERRITORIES. 106 km N of Chan Lake, S of Edzo, 2208.

E. ACRIS L. ssp. POLITUS (Fr.) Schinz & Keller. $2n = 18$. UNITED STATES. ALASKA. Alaska Hwy, MP287, 2 km W of Shaw Creek, *2445*.

E. AUREUS Greene. $2n = 18$. CANADA. ALBERTA. Plateau Mountain, *204, 201*.

E. CAESPITOSUS Nutt. $2n = 18$. CANADA. ALBERTA. Exshaw, *851*; Rosedale, *667*. $2n = 27$. CANADA. ALBERTA. Rosedale, *676*.

E. COMPOSITUS Pursh. $2n = 54$. CANADA. ALBERTA. Highwood, *586*; Longview, *150, 566*; Pincher Creek, *544*. BRITISH COLUMBIA. Princeton, *327*. UNITED STATES. ALASKA. Alaska Hwy MP287, 2 km W of Shaw Creek, *2443*.

E. CORYMBOSUS Nutt. $2n = 18$. CANADA. BRITISH COLUMBIA. Kamloops, *623*; Princeton, *323*.

E. DIVERGENS Torr. & Gray. $2n = 27$. CANADA. BRITISH COLUMBIA. Princeton, *328*.

E. FILIFOLIUS Nutt. $2n = 18$. CANADA. BRITISH COLUMBIA. Merritt, *336*.

E. GLABELLUS Nutt. $2n = 18$. CANADA. ALBERTA. Cataract Creek, *181*; Banff National Park, *847*; Exshaw, *849*; Redwood Meadows, *440, 439*.

E. GLABELLUS Nutt. ssp. PUBESCENS (Hook.) Cronq. $2n = 36$. CANADA. ALBERTA. Millarville, *655*. $2n = 36 + b$; Elkwater Provincial Park, *691*. $2n =$ ca 50; Longview *580*.

E. HUMILUS Grah. $2n = 36$. CANADA. BRITISH COLUMBIA. Queen Mt., *488*. NORTHWEST TERRITORIES. Hwy 3, 24 km W of Pump Station 8, S of Yellowknife, *2199*. YUKON. Dempster Hwy, KP155, 38 km S of Engineer Creek, *2638*.

E. HYSSOPIFOLIUS Michx. $2n = 18$. UNITED STATES. ALASKA. Glenn Hwy, 38 km NE of Nebesna Junction, *2548*.

E. OCHROLEUCUS Nutt. $2n = 18$. CANADA. ALBERTA. Rosedale, *670*.

E. PERIGRINUS (Pursh) Greene. $2n = 18$. CANADA. ALBERTA. Plateau Mountain, *217, 369*; 2.2 mi from turnoff to Plateau Mountain, *219*; Kananaskis Provincial Park, *1122*. BRITISH COLUMBIA. Mt. Ethelbert, *489*; Glacier National Park, *595*; Brooks Peninsula, Cassiope Pond, *UAC39641*; Brooks Peninsula, Cape Cook Lagoon, *UAC39642*.

E. PHILADELPHICUS L. $2n = 18$. CANADA. BRITISH COLUMBIA. Bridal Veil Fall Provincial Park, *285*; Mt. Revelstoke National Park, *608*. ONTARIO. Wrigley's Corners, *6, 12*. *SASKATCHEWAN. North Saskatchewan River, 508, 509*.

E. PUMILUS Nutt. $2n = 18$. CANADA. BRITISH COLUMBIA. Princeton, *329*.

E. SPECIOSUS (Lindley) DC. $2n = 18$. CANADA. BRITISH COLUMBIA. Manning Provincial Park, *320*.

E. SUBTRINERVIS Rydb. var. CONSPICUUS (Rydb.) Cronq. $2n = 18$. CANADA. ALBERTA. S of Livingston Falls, *1114*. BRITISH COLUMBIA. between Kelowna and Vernon, *640*; W of Manning Provincial Park, *301*; Midway, *1074*.

FRANSERIA CHAMISSONIS Less. $2n = 18$. CANADA. BRITISH COLUMBIA. Brooks Peninsula, mouth of Cape Cook Lagoon, *no voucher.*.

GAILLARDIA ARISTATA Pursh. $2n = 34$. CANADA. BRITISH COLUMBIA. Merritt, *626*.

GNAPHALIUM VISCOSUM HBK. $2n = 28$. CANADA. BRITISH COLUMBIA. 30 km S of Kelowna, *1061*.

HAPLOPAPPUS LYALLII A. Gray. $2n = 18$. CANADA. ALBERTA. Plateau Mountain, *205*.

HETEROTHECA VILLOSA (Pursh) Shinn. $2n = 18$. CANADA. ALBERTA. Canmore to Exshaw, *257*.

HIERACIUM ALBIFLORUM Hook. $n = 9$. CANADA. Brooks Peninsula, mouth of Cape Cook Lagoon, *no voucher.* $2n = 18$. BRITISH COLUMBIA. Kamloops to Jasper, *828*; Kamloops, *612A*.

H. CANADENSE Michx. $2n = 27$. CANADA. ALBERTA. N of Drayton Valley, *501*.

H. UMBELLATUM L. $2n = 27$. CANADA. ALBERTA. Athabasca sand dunes, *AD4*,

HYMENOXYS RICHARDSONII (Hook.) Cockerell. $2n = 30$. CANADA. ALBERTA. Drumheller, *428*; Pincher Creek, *539*.

MACHAERANTHERA CANESCENS (Pursh) A. Gray. $2n = 8$. CANADA. ALBERTA. Newell County limit, *960*.

PRENANTHES ALATA (Hoo,.) D. Dietr. $n = 8$. CANADA. BRITISH COLUMBIA. Brooks Peninsula, mouth of Cape Cook Lagoon, *no voucher.*

SENECIO CONGESTUS (R. Br.) DC. $2n = 48$. CANADA. ALBERTA. Rosedale to Hanna, *677*.

S. CYMBALARIOIDES Bueck. $2n = 44$. CANADA. ALBERTA. Crowsnest Creek, *554*.

S. INDECORUS Greene $2n =$ ca 70. CANADA. BRITISH COLUMBIA. Glacier National Park, *600A*.

S. LUGENS Rich. $2n = 80$. CANADA. ALBERTA. Crowsnest Creek, *468*.

S. TRIANGULARIS Hook. $2n = 40$. CANADA. BRITISH COLUMBIA, Creston, *1084*.

SOLIDAGO CANADENSIS L. $2n = 18$. UNITED STATES. ALASKA. Alaska Hwy, MP287, 2 km W of Shaw Creek, *2441*.

S. MISSOURIENSIS Nutt. $2n = 36$. CANADA. ALBERTA. Rosedale, *663*.

S. MULTIRADIATA Ait. $2n = 18$. CANADA. YUKON. Top of the World Hwy, KP42, northern Dawson Range, 42 km W of Dawson, *2467*. UNITED STATES. ALASKA. Denali Hwy, Windy Creek, Gracious Lodge, *2387*. $2n = 36$. CANADA. BRITISH COLUMBIA. Muncho Lake Provincial Park, Strawberry Fields Campground, *2239*; Haines Hwy, Chilkat Pass, 1 km N of Stanley Creek, *2524*. NORTHWEST TERRITORIES. 20 km NW of Edith Creek, 11 km NW of Lake Creek Campground, KP865, *2487*; Richarson Hwy, KP21, *2620*; 10 km N of Caribou Lake Campground, turnofff from Dempster Hwy, *2633*; Happy Valley Campground, *2634*. YUKON. Campbell Hwy, Bruce Lake near Ross River, *2275*; Campbell Hwy, 3 km W of Ross River, *2308*; Dempster Hwy, KP155, 38 km S of Engineer Creek Campground, *2637*; Dawson, *2473*; Dempster Hwy, southern Ogilvie Mtns., just N of survival shack, *2481*; Dempster Hwy, Engineer Creek Campground, *2586*; Kluane National Park, Kascawulch Glacier Trail, *2569*; Dempster Hwy, KP83, 4 km N of survival shack, 11 km N of Tombstone Mtn Campground, *2651*; 21 km S of crossing of Dempster Hwy, and Klondike Loop, on the Klondike Loop, *2658*. UNITED STATES. ALASKA. Steese Hwy, 2 km NE of Captain Creek, 8 km NE of campground and Aurora Borealis Research Station, *2396*; Glenn Hwy, MP107, 55 km NE of Slara, *2544*; Alaska Hwy, scenic viewpoint, MP1400, 13 km NW of Gerstle River, *2448*; Glenn Hwy, 42 km NE of Slara, *2547*; Denali Hwy, 7 km W of Paxson, *2569*.

TANACETUM HURONENSE Nutt. $2n = 54$. CANADA. ALBERTA. Athabasca sand dunes, *no voucher*.

T. VULGARE L. $2n = 18$. CANADA. BRITISH COLUMBIA. Okanagan Valley, Salmon Arm turnoff, *no voucher*.

BORAGINACEAE

LITHOSPERMUM INCISUM Lehm. $2n = 36$. CANADA. ALBERTA. Pincher Creek, *540*.

MERTENSIA PANICULATA (Ait.) G. Don. $2n = 48$. CANADA. ALBERTA. Calgary, Edworthy Park, *431*.

BRASSICACEAE

CAKILE EDENTULA (Bigel.) Hook. $n = 9$. CANADA. BRITISH COLUMBIA. Brooks Peninsula, Cape Cook Lagoon, *no voucher*.

DRABA OLIGOSPERMA Hook. $2n = 32$. CANADA. ALBERTA. Plateau Mountain, *585*.

PHYSARIA DIDYMOCARPA (Hook.) A. Gray. $2n = 16 + 2B$. CANADA. ALBERTA. Redwood Meadows, *562*.

CARYOPHYLLACEAE

STELLARIA HUMIFUSA Rottb. $2n = 26$. CANADA. BRITISH COLUMBIA. Brooks Peninsula, Cape Cook Lagoon, *UAC39629*.

S. LONGIPES Goldie. $2n = 52$. CANADA. ALBERTA. Calgary, *223*; Exshaw, *530*; Longview, *569*; Plateau Mountain, *202, 366*. $2n = 78$; Calgary, *648*; Canmore to Exshaw, *249*. BRITISH COLUMBIA. Manning Provincial Park, *315*; Tillery Rd, *335*. $2n = 104$; Kamloops, *617*.

CYPERACEAE

CAREX CIRCINATA C. A. Meyer. $2n =$ ca 58. CANADA. BRITISH COLUMBIA. Brooks Peninsula, Gentiana Lake, *UAC39622*.

DROSERACEAE

DROSERA ROTUNDIFOLIA L. $2n = 20$. CANADA. BRITISH COLUMBIA. Brooks Peninsula, Gentiana Lake, *UAC 39630*.

ERICACEAE

GAULTHERIA SHALLON Pursh. $n = 22$. CANADA. BRITISH COLUMBIA. Brooks Peninsula, Cassiope Pond, *no voucher*.

VACCINIUM ULIGINOSUM L. $2n = 24$. CANADA. BRITISH COLUMBIA. Brooks Peninsula, Cassiope Pond, *UAC39636*.

FABACEAE

ASTRAGALUS DECUMBENS (Nutt.) A. Gray var. serotinus (A. Gray) Barneby. $2n = 18$. CANADA. ALBERTA. Canmore to Exshaw, *248*.

LUPINUS NOOTKATENSIS Donn ex Sims. $n = 24$. CANADA. BRITISH COLUMBIA. Brooks Peninsula, Harris Peak, *no voucher*.

VICIA GIGANTEA Hook. $n = 7$. CANADA. BRITISH COLUMBIA. Brooks Peninsula, Cape Cook Lagoon, *no voucher*.

HYDROPHYLLACEAE

PHACELIA LINEARIS (Pursh) Holzinger. $2n = 22$. CANADA. BRITISH COLUMBIA. Kamloops, *622*.

P. SERICEA (Grah.) A. Gray. $2n = 22$. CANADA. ALBERTA. Calgary, Fish Creek, *652*.

JUNCACEAE

JUNCUS FALCATUS E. Meyer. $2n =$ ca 40. CANADA. BRITISH COLUMBIA. Brooks Peninsula, mouth of Cape Cook Lagoon, *UAC39624*.

LILIACEAE

ALLIUM CERNUUM Roth. $2n = 14+6$-11B's. CANADA. BRITISH COLUMBIA. Brooks Peninsula, Quineex, *no voucher.*

FRITILLARIA CAMSCHATCENSIS (L.) Ker-Gawl. $2n = 24$. CANADA. BRITISH COLUMBIA. Brooks Peninsula, Gentiana Lake, *UAC39625.*

SMILACINA RACEMOSA (L.) Desf. $2n = 36$. CANADA. ALBERTA. Drumheller, *419.*

S. STELLATA (L.) Desf. $2n = 36$. CANADA. ALBERTA. Calgary, University of Calgary campus, *424.* $2n = 54$. CANADA. ALBERTA. Calgary, Edworthy Park, *421.*

STENANTHIUM OCCIDENTALE A. Gray. $2n = 16$. CANADA. BRITISH COLUMBIA. between Banff and Radium, *1147.*

TOFIELDIA GLUTINOSA (Michx.) Pers. $2n = 30$. CANADA. BRITISH COLUMBIA. Golden, *590*; Brooks Peninsula, Cassiope Pond, *UAC39626.*

VERATRUM ESCHSCHOLTZII A. Gray. $n = 16$. CANADA. BRITISH COLUMBIA. Brooks Peninsula, Cassiope Pond, *no voucher.*

ORCHIDACEAE

HABENARIA CHORISIANA Cham. $n = 21$. CANADA. BRITISH COLUMBIA. Brooks Peninsula, Cape Cook Lagoon, *UAC39627.*

H. HYPERBOREA (L.) R. Br. $2n = 42$. CANADA. ALBERTA. Canmore to Exshaw, *529.*

PLANTAGINACEAE

PLANTAGO ERIOPODA Torrey. $2n = 24$. CANADA. ALBERTA. Drumheller, *525.*

P. PURSHII R. & S. $2n = 20$. CANADA. BRITISH COLUMBIA. Princeton, *639.*

POACEAE

DESCHAMPSIA CAESPITOSA (L.) Beauv. $n = 13$. CANADA. BRITISH COLUMBIA. Brooks Peninsula, Gentiana Lake, *UAC39167.*

MELICA SUBULATA (Griseb.) Scribn. $2n = 18$. CANADA. BRITISH COLUMBIA. Brooks Peninsula, Cassiope Pond, *UAC39620.*

PUCCINELLIA NUTKAENSIS (Presl.) Fern. & Weath. $2n = 56$. CANADA. BRITISH COLUMBIA. Brooks Peninsula, Cassiope Pond, *UAC39621.*

RANUNCULACEAE

ANEMONE PARVIFLORA Michx. $2n = 16$. CANADA. ALBERTA. Redwood Meadows, *128.*

RANUNCULUS REPENS L. $2n = 32$. CANADA. BRITISH COLUMBIA. Creston, *1086*.

ROSACEAE

POTENTILLA PENSYLVANICA L. $2n = 28$. CANADA. ALBERTA. Longview, *576*.

SAXIFRAGACEAE

HUECHERA FLABELLIFOLIA Rydb. $2n = 14$. CANADA. ALBERTA. Pincher Creek, *547*.

H. GLABRA Piper. $n = 7$. CANADA. BRITISH COLUMBIA. Brooks Peninsula, Cape Cook lagoon, *UAC39631*.

SCROPHULARIACEAE

PEDICULARIS ORNITHORHYNCHA Benth. in Hook. $2n = 16$. CANADA. BRITISH COLUMBIA. Brooks Peninsula, Cassiope Pond, *UAC39637*.

PENSTEMON ALBIDUS Nutt. $2n = 14$. CANADA. SASKATCHEWAN. intersection of Hwy 271 and Hwy 615, *989*.

VALERIANACEAE

VALERIANA SEPTENTRIONALIS Rydb. $2n = 16$. CANADA. ALBERTA. Hwy 6, to Waterton, *552*.

DISCUSSION

Chromosome numbers were determined for 183 individuals representing 93 taxa in 53 genera from western North America. The majority of these counts are diploid, however some taxa are represented by triploid or higher ploidy levels. Since these counts do not reflect exceptions for these taxa and support previous reports they are presented without comment.

Of the 93 taxa examined, chromosome numbers are available for 29 taxa from the Brooks Peninsula. The proximity of the Brooks Peninsula on the west coast of Vancouver Island to the glacial refugium of the Queen Charlotte Islands has led to the supposition that the former may also have been a refugial area during glacial times. Polyploid taxa typically colonize formerly glaciated regions (Packer 1971) whereas in a refugial area taxa represented by the diploid cytotype, or lower level polyploids should predominate. Thus, if a taxon is represented by multiple cytotypes the distribution of the diploid cytotype should reflect the approximate limits of the refugial area in which they survived (Randhawa and Beamish 1972). Five species (*Artemisia trifurcata* Stephan. ex Sprengel., *Franseria chamis-*

sonis Less., *Gaultheria shallon* Pursh, *Melica subulata* (Griseb.) Scribn., and *Vaccinium uliginosum* L.) are reported as diploid in this region, whereas elsewhere in British Columbia they occur as polyploids. These results support the theory that the Brooks Peninsula was a refugial area during glacial times, but further multidisciplinary studies are necessary before this theory is accepted.

ACKNOWLEDGMENTS

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NOTES

NOTES ON *PEPEROMIA HETERODOXA* (PIPERACEAE) IN MÉXICO.—Fieldwork in southern México during 1983 yielded a sterile sample of an unusual small succulent. Following cultivation, this plant produced flowering spikes typical of the genus *Peperomia* and was subsequently determined as *P. heterodoxa* Standley and Steyermark. A return visit to the collection site during 1985 confirmed that this species is locally common and allowed us to supplement greenhouse observations on its life cycle. *Peperomia heterodoxa* was described by Standley and Steyermark (1952) based on a single specimen:

GUATEMALA. HUEHUETENANGO: Sierra de los Cuchumatanes, between Santa Ana Huista and Rancho Lucas, elev. 800 – 900 m, 26 Aug 1942, *Steyermark 51340* (HOLOTYPE: F!).

Collection data for our specimens are:

MÉXICO. OAXACA: 2 km N of bridge at Juchatengo on Hwy 131 from Pto. Escondido, elev. 900 m, 28 Dec 1983, *Yatskievych, Windham, and Ranker 83-455* (ENCB); same locality, 18 Jul 1985, *Yatskievych, González L., Ranker, Starr, and Starr 85-198* (ARIZ, CHAPA, IND, UTEP).

Our collections represent the second known population of this species and a range extension of ca 600 km westward from the type locality.

At our site the species is locally common on steep shale slopes in ravines and is part of the dense and diverse understory of a seasonal forest association (bosque tropical caducifolio, *sensu* Rzedowski 1978). Dominants include *Bursera, Acacia, Ficus*, and several columnar cacti. Data from climatological stations at other locations in central and southern Oaxaca (García 1965) indicate that the site receives ca 70 – 80 cm annual rainfall, with a pronounced rainy season from late April to mid October.

Plants from Oaxaca agree in all respects with Standley and Steyermark's (1952) detailed description of the species from Guatemala. The species is notable for its very slender spikes (Fig. 1a, c) and high degree of leaf dimorphism (Fig. 1a). During the dry season plants consist of relatively stout, unbranched aerial stems with regular whorls of 5 – 7 appressed, small, orbicular, highly succulent leaves (Fig. 1a, b). These have translucent greenish adaxial "window" surfaces (a common feature of the genus) and dark reddish undersides.

With the onset of rains, these lower leaves spread, existing internodes elongate, and rapid, branching, apical growth is initiated, with larger,

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[1]Present address: Missouri Botanical Garden, P.O. Box 299, St. Louis, MO 63166, U.S.A.

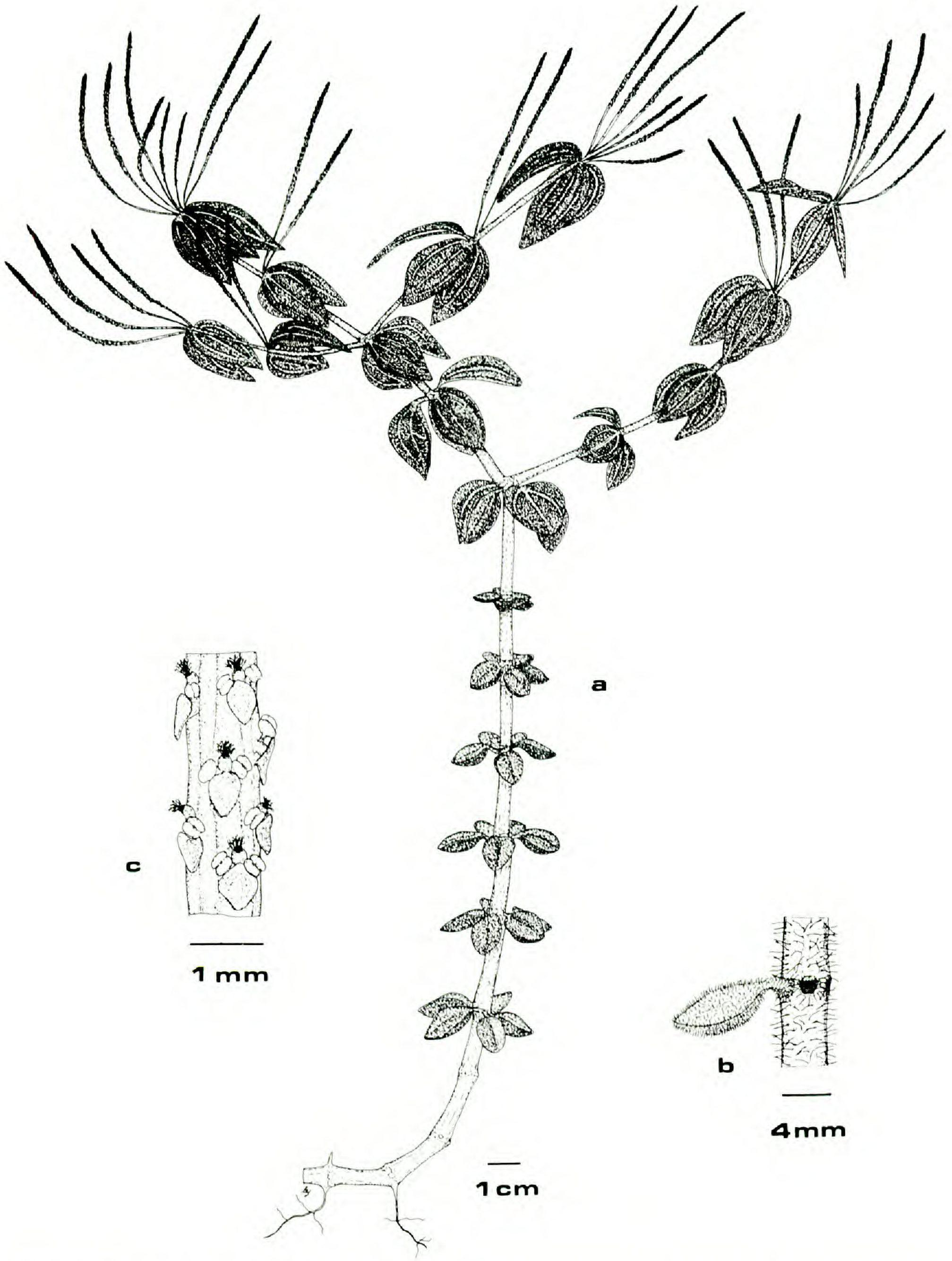

FIG. 1. *Peperomia heterodoxa*. a, habit, showing leaf dimorphism and position of inflorescences. b, detail of lower node, with succulent leaf and leaf scars. c, median portion of flowering spike.

ovate, green, nonsucculent leaves, 3 – 5 per whorl (Fig. 1a). Flowering spikes occur in the upper leaf axils and in terminal whorls, and are produced during portions of June and July. Concurrently with anthesis and fruiting, new succulent aerial shoots develop from meristems near adventitious roots of the horizontal to ascending, underground basal portions of each old stem. These new shoots cease growth at the end of the rainy season, by which time fruits have matured. The original stems and leaves die back slowly through a progressive disarticulation of terminal nodes, leaving only the new season's succulent growth.

In the greenhouse, year-round watering eliminates the dormancy period between the succulent and herbaceous portions of the life cycle, as well as delaying fall senescence. Well-watered plants also exhibit shorter internodes and less pubescence than specimens studied in the field. We have not been successful at attempts to vegetatively propagate the species using stem and leaf cuttings in a variety of soil mixtures, and self-pollinated plants fail to set seed. Small succulent plantlets are sometimes produced (in the greenhouse) from axillary meristems of upper leaves after die-back has already begun. Such plantlets readily root and grow following disarticulation from the main stem. This phenomenon has not been observed in nature, however, and its importance in the vegetative propagation of plants in the wild may be minimal.—*George Yatskievych*[1] *and Lewis E. Johnson, Department of Biology, Indiana University, Bloomington, IN 47405, U.S.A.*

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FIVE ADDITIONS TO THE TEXAS FLORA—*Uvularia perfoliata* L. (Liliaceae) is a perennial, herbaceous and colonial species with long underground stolons. It is generally observed as scattered clumps of plants in moist rich woods, wooded coves and alluvial woods (Gleason 1968, Radford et al. 1968). *Uvularia perfoliata* has been collected from a mesic wooded creek bottom in central east Texas in Sabine County (*Nixon 14347* ASTC, SMU). Brown (1972) reported its occurrence in Texas but we are unaware of its documentation. This bellwort is known from two counties in west central Arkansas (Smith 1978) and from Louisiana (MacRoberts 1984), so its presence in Texas is not surprising.

MICROSTEGIUM VIMINEUM (Trin.) A. Camus (Poaceae) is native to Asia and adventive in the eastern United States west to Louisiana and Arkansas (Hitchcock 1951; Allen 1980; MacRoberts 1984; Smith 1978). This grass is a decumbent, branched, and matted annual which roots from the lower nodes. It was recently collected on a moist wooded hillside above Tanyard Creek in Bowie County (*McCrary 1097* ASTC, SMU).

GLYCERIA ARKANSANA Fern. (Poaceae) is reported for Texas by Hitchcock (1951) but Correll and Johnston (1970), Correll and Correll (1975), and Gould (1975) apparently examined no Texas specimens. A recent collection (*McCrary and Tidwell 1176* ASTC, SMU) from a shallow creek in Bowie County verifies its presence in the state. This aquatic grass is also present in the adjacent states of Oklahoma, Arkansas, and Louisiana (Correll and Correll 1975; MacRoberts 1984; Smith 1978).

VERBENA SIMPLEX Lehm. is a slender upright, narrow leaved, perennial vervain which usually grows on dry soils of woods and roadsides (Gleason 1968). It is widespread in the eastern United States southwest to Oklahoma and Arkansas (Gleason 1968). A collection from Red River County (*McCrary 1016* ASTC, SMU) in northeast Texas near Oklahoma is the first for Texas.

[10]VICIA TETRASPERMA (L.) Moench, is an annual European legume naturalized along roadsides in the eastern United States west to Wisconsin, Missouri, and Texas (Gleason 1968; Steyermark 1975). Although reported by these authors as occurring in Texas, we are not aware of its verified existence. This taxon is present in Louisiana and evidently has spread rapidly in Texas. It was collected in Walker, Trinity, Anderson and Morris counties in 1984 (*Nixon 13333, 13435, 13536*, and *13672* ASTC, SMU) and in Cherokee (*Nixon 14702* ASTC) and Smith (*Nixon 14449* ASTC) counties in 1985.

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VERIFICATION OF *ASARUM CANADENSE* L. (ARISTOLOCHIACEAE) IN LOUISIANA—A population of *Asarum canadense* L. covering about 400 square meters was discovered in rich mesic woods of the Tunica Hills in West Feliciana Parish, Louisiana. Specimens were collected on private property (ca 5 mi NW of the jct of La Hwys 968 and 66, T1S, R4W, Sec. 47) in the vegetative condition on 17 July 1986 (*L. E. Urbatsch et al. 4107*, LSU) and in flower on 3 April 1987 (*Patricia B. Cox et al. 4977*, LSU). The *Asarum* was growing on a colluvial bench above Polly Creek at the base of a west-facing bluff in association with *Acer negundo* L., *Adiantum pedatum* L., *Fagus grandiflora* Ehrh., *Halesia diptera* Ell., *Lindera benzoin* (L.) Blume, and *Quercus michauxii* Nutt.

One specimen in the Tulane University Herbarium collected by Joshiah Hale (1791 – 1856) bears a Flora of Louisiana label but gives neither locality nor temporal data. According to Steyermark (1963) wild ginger is distributed from New Brunswick to Ontario south to North Carolina, Arkansas, and Kansas. The population nearest the one under consideration occurs ca 150 km northeast in Cophiah Co., Mississippi (Mississippi Natural Heritage Program). About 20 other sites from the northern half of Mississippi are known. In Arkansas *Asarum* has been documented from Polk and Phillips counties northward (Smith 1978).

The flora of the Tunica Hills in southwestern Mississippi and adjacent Louisiana includes many Appalachian Pleistocene relict species. A few of these are *Actea pachypoda* Ell., *Circaea latifolia* Hill, *Corallorhiza odontorhiza* (Willd.) Nutt., *Diplazium acrosticoides* (Sw.) Butler, *Pachysandra procumbens* Michx., and *Panax quinquefolius* L. (Allen et al. 1975).—*Patricia B. Cox, Lowell E. Urbatsch, and Elizabeth M. Harris, Department of Botany and Albert Meier School of Forestry, Wildlife, and Fisheries, Louisiana State University, Baton Rouge, LA 70803, U.S.A.*

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TRIDENS × *OKLAHOMENSIS (T. FLAVUS* × *T. STRICTUS)* (POACEAE) NEW TO LOUISIANA—*Tridens oklahomensis* (Feath.) Chase was initially described from collections made near Stillwater, Oklahoma, by Featherly (1938) who remarked on its similarity to *T. flavus* (L.) Hitchc. Subsequently, Kucera (1957) reported this grass from Boone County, Missouri, and suggested it to be an interspecific hybrid between *T. flavus* (L.) Hitchc. and *T. strictus* (Nutt.) Nash. Later field and laboratory studies provided evidence that *T. oklahomensis* is indeed a hybrid (Crooks and Kucera 1973). A third location for *T.* × *oklahomensis* was reported for Butler County, Missouri, ca 300 km south of the original site in that state (Schuckman and Kucera 1984).

On 18 October 1986, three clumps of *T.* × *oklahomensis* were discovered at the Idlewild Experiment Station about two miles south of Clinton, Louisiana, in East Feliciana Parish. Vouchers (*McKenzie et al.* 555) are deposited in LSU, FLAS, LAF, OKLA, MO, NLU, TAES, UMO, and US. On 3 November 1986, we returned to the site and located 21 additional clumps in a meadow and roadside adjacent to the original discovery site. The clumps were scattered along a slight elevational gradient which ranged from fairly dry to moist. The hybrids appeared to produce mostly malformed nonstaining (aniline blue in lactophenol) pollen and no mature caryopses were observed. Their morphological features were like those described by Crooks and Kucera (1973). Both *T. flavus* and *T. strictus* were observed in the area, but the former was far more abundant than the latter. *Tridens* × *oklahomensis* is not reported for Louisiana by Allen (1980) and these collections constitute the first record for this state and the fourth report of its occurrence.

The author citation generally given for *T.* × *oklahomensis* (Feath.) Feath. apparently should be "(Feath.) Chase" or "(Feath.) Feath. ex Chase." The combination is attributed to Featherly in the second edition of Hitchcock's manual by Chase who is the publishing author (Chase 1951).—*Paul M. McKenzie, Louisiana Cooperative Fish and Wildlife Unit, Lowell E. Urbatsch and Damon E. Waitt, Department of Botany, Louisiana State University, Baton Rouge, LA 70803-1705, U.S.A.*

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ADDITIONS TO THE FLORA OF WEST VIRGINIA—Eight taxa are reported new for the state of West Virginia. *Eleocharis elliptica* Kunth, *Carex lupuliformis* Sartwell, *Juncus canadensis* La Harpe forma *conglobatus* Fern., *Acnida altissima* Riddell, and *Spermacoce glabra* Michaux are doubtless natives, while *Rhynchospora fusca* Aiton f., *Anoda cristata* (L.) Schldl., and *Ludwigia peploides* (Kunth) Raven subsp. *glabrescens* (Kuntze) Raven are presumably adventives. Voucher specimens are on file at the Marshall University herbarium (MUHW).

ELEOCHARIS ELLIPTICA Kunth—GREENBRIER CO.: Meadow River wetlands near Crawley, 19 Jun 1984, *Brant 490* (MUHW), and 14 Jul 1984, *Brant & Zappia 497* (MUHW). This tall, slender spikerush was collected from two separate localities within the Meadow River wetlands, both from open circumneutral, spring-fed emergent wetland. The sites are permanently saturated by springs (minerotrophic) and are never inundated by stream water. Associated species include *Isoetes engelmannii* A. Br., *Eleocharis tenuis* (Willd.) Schult., *Symplocarpus foetidus* (L.) Nutt., *Acorus calamus* L., *Juncus tenuis* Willd., *J. dudleyi* Wieg., *Spiraea alba* Du Roi, *Sanguisorba canadensis* L., *Rosa palustris* Marsh., *Pedicularis lanceolata* Michaux, and *Campanula aparinoides* Pursh. The distribution of *E. elliptica* is generally northern, occurring from Newfoundland to British Columbia in the north, southward to New Jersey, Pennsylvania, Ohio, southern Indiana, southern Illinois, and Iowa (Fernald, 1950). For current treatments of this taxon see Voss (1972), and especially Drapalik & Mohlenbrock (1960, 1961).

RHYNCHOSPORA FUSCA (L.) Aiton f.—GREENBRIER CO.: Meadow River wetlands near Crawley, 25 Jul 1983, *Brant & Lycan 309* (MUHW), and 1 Oct 1983, *Brant & Meadows 445, 448* (MUHW). *Rhynchospora fusca* is restricted to circumneutral seeps emerging from Mississippian-age

calcareous shales at the three localities from which these collections were made. Voss (1972) notes that in Michigan, *R. fusca* is often found in somewhat "marly" places. Associated species include *Osmunda cinnamomea* L., *Dichanthelium sphaerocarpon* (Ell.) Gould, *Eleocharis tenuis*, *Carex debilis* Michx., *Spiraea alba*, and *Rosa palustris*. This beaked-rush is a northern and coastal plain species distributed in the north from Newfoundland and Nova Scotia to Ontario, south to Delaware and Michigan (Fernald 1950). Its occurrence at higher elevations (2,400 + feet) in West Virginia is unexpected and may represent a disjunct population; however, collections identified as *R. fusca* from Florida and Georgia are represented in the Herbarium of the Missouri Botanical Garden (MO). It is possible that *R. fusca* was introduced into West Virginia in hay mixtures or cattle feed; however, each of the three sites represented by these collections is at approximately the same elevation, and each site is in a different watershed and well above present inundations by its stream. This suggests that these are long-established colonies.

CAREX LUPULIFORMIS Sartwell—GREENBRIER CO.: Meadow River wetlands near Crawley, 2 Sep 1983, *Brant & Williams 424* (MUHW), and 16 Sep 1983, *Brant 437, 442* (MUHW). This showy sedge is found in frequently inundated openings of scrub/shrub emergent wetland along the Meadow River. It is most abundant in permanently saturated depressions left by past meanders. Associated species include *Carex lupulina* Willd., *C. tuckermanii* Dewey, *C. typhina* Michx., *C. squarrosa* L., *C. grayii* Carey, *C. vesicaria* L., *C. bromoides* Willd., *C. stricta* Lam., *C. stipata* Willd., *Dulichium arundinaceum* (L.) Britton, *Sparganium eurycarpum* Engelm., *S. americanum* Nutt., *Leersia oryzoides* (L.) Swartz, *Panicum rigidulum* Nees, *Polygonum hydropiperoides* Michx., *Acer rubrum* L., *Nyssa sylvatica* Marsh., *Rosa palustris*, *Alnus serrulata* (Ait.) Willd., and *Cephalanthus occidentalis* L. The distribution of *C. lupuliformis* is from southern Quebec, southern Ontario to Minnesota in the north, south to Connecticut, Virginia, Florida, Louisiana, and eastern Texas (Fernald 1950; Reznicek & Ball 1974). It should occur elsewhere in West Virginia, especially in calcareous situations. When mature it is readily separated from the more common *C. lupulina* by its narrower pistillate spikes, spreading perigynia, and distinctively knobbed achenes. The chromosome number of *C. lupuliformis*, $2n = 60$, also differs from *C. lupulina*, $2n = 56$ (Reznicek & Ball 1974).

JUNCUS CANADENSIS La Harpe forma CONGLOBATUS Fern.—GREENBRIER CO.: Otter Creek floodplain, Meadow River wetlands near Crawley, 16 Sep 1983, *Brant 438* (MUHW). This form was collected

from a single locality in frequently inundated open emergent wetland associated with *Dulichium arundinaceum, Eleocharis smallii* Britton, *Scirpus cyperinus* (L.) Kunth, *Carex lupulina, C. vulpinoidea* Michaux, *Juncus effusus, Panicum rigidulum, Glyceria canadensis* (Michaux) Trin., *Lysimachia terrestris* (L.) BSP., and *Vernonia novaboracensis* (L.) Michaux. The form is primarily coastal, but occurs locally inland from Maine to Minnesota and south to Georgia and northern Illinois (Fernald 1950).

AMARANTHUS TUBERCULATUS (Moq.) Sauer (*Acnida altissima* Riddell var. *altissima*)—CABELL CO.: Sand/mud flats of the Ohio River ca 2 mi south of Lesage, 9 Oct 1983, *Brant & Zappia 449* (MUHW). This species of water-hemp is a locally abundant element of the mud/sand flat flora of the Ohio River, often associated with *Eragrostis hypnoides* (Lam.) BSP., *Ammannia coccinea* Rottb., *Ludwigia decurrens* Walt., *L. leptocarpa* (Nutt.) Hara, and *Rotala ramoisior* (L.) Koehne. *Acnida altissima* is distributed from Ontario to Colorado in the north, south to Kentucky, Indiana, Illinois, and Missouri, and is adventive to New England (Fernald 1950).

ANODA CRISTATA (L.) Schldl. var. CRISTATA—CABELL CO.: Sand/mud flats of the Ohio River ca 2.5 mi above Guyandotte, 30 Sep 1983, *Brant & Zappia 444* (MUHW). This colony was associated with *Eragrostis hypnoides, Panicum dichotomiflorum* Michaux, *Arthraxon hispidus* (Thunb.) Makino, *Ludwigia decurrens*, and *L. leptocarpa*. I have observed another colony about 5 miles upstream. This mallow is native to the southwestern U.S. and Mexico, and is apparently becoming more widely established in the east. Fernald (1950) gives its distribution as southeast Pennsylvania, Iowa, and Missouri to Texas. It has also been collected in Hancock and Massac counties in Illinois (Mohlenbrock 1975), where it has allegedly escaped from cultivation.

LUDWIGIA PEPLOIDES (Kunth) Raven subsp. GLABRESCENS (Kuntze) Raven (*Jussiaea repens* L. var. *glabrescens* Kuntze)—CABELL CO.: Ohio River ca 2 mi south of Lesage, 9 Oct 1983, *Brant 451* (MUHW). In West Virginia, *L. peploides* occurs on the sand/mud flats of the Ohio River, usually at the waters edge, but also in open springy areas on the flats often associated with *Eragrostis hypnoidea* and *Eclipta alba* (L.) Hassk. I have observed several colonies along the Ohio River, often forming large, spreading mats. This species is widely distributed in the east and is apparently spreading. For the current taxonomy, see Raven (1963).

SPERMACOCE GLABRA Michaux—CABELL CO.: Ohio River ca 2 mi north of Guyandotte, 8 Sep 1984, *Brant 527* (MUHW). This buttonweed was collected from a springy, semi-open area on the upper sand/mud flats of

the Ohio River. Associated species include *Samolus parviflora* Raf., *Diodia virginiana* L., and *Eclipta alba*. *Spermacoce glabra* is distributed in the south from Florida to Texas, north to southern Ohio, southern Indiana, southern Illinois, Missouri, and southeast Kansas (Fernald 1950). Southwestern West Virginia is at the northeastern limits of its range.

ACKNOWLEDGMENTS

Acknowledgment is kindly extended to friends and colleagues (mentioned in the text) who accompanied and assisted in the field, Roy Gereau and Ann O'Donnell for their superb editing and invaluable suggestions, Susan Meister and Diana Winkelmeyer for their expert word processing, and Dan K. Evans for providing impetus, confirmations, and much, much more. The Greenbrier County collections were made in conjuction with floristic studies in the Meadow River wetlands. The study comprised partial fulfillment of the Master of Science degree and travel expenses were, in part, defrayed by Marshall University, Huntington, West Virginia.—*Alan E. Brant, Herbarium Assistant, Missouri Botanical Garden, P.O. Box 299, St. Louis, MO 63166-0299.*

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ANNOUNCEMENT

The George R. Cooley Award for 1987 was presented to Robert Wyatt of the University of Georgia, Athens, for his paper co-authored with Ireneusz J. Odrzykoski and Ann Stoneburner entitled "Allopolyploidy in bryophytes: recurring origins of *Plagiomnium medium*." The award is given annually by the American Society of Plant Taxonomists for the outstanding contributed paper in plant systematics presented at the annual meeting.

The fourth Asa Gray Award was presented to Reed C. Rollins of Harvard University, Cambridge, Massachusetts. The Asa Gray Award is given by the American Society of Plant Taxonomists to honor an individual "for outstanding accomplishments pertinent to the goals of the Society." The award has been presented to Rogers McVaugh at the 1984 meeting, Arthur Cronquist at the 1985 meeting, and Lincoln Constance at the 1986 meeting.

MISSOURI BOTANICAL GARDEN DIRECTOR RECEIVES CARR MEDAL AT UNIVERSITY OF FLORIDA

Gainesville, Fl., May 22, 1987—Dr. Peter Raven, director of the Missouri Botanical Garden, was recently awarded the Archie F. Carr Medal at the University of Florida (UF). Raven is the third recipient of the medal, which recognizes outstanding national and international contributions to the knowledge and understanding of man's natural heritage.

Under Raven's direction, the Missouri Botanical Garden's tropical botany studies program has become one of the most active in the world. Raven is also chairman of the National Museum Services Board and home secretary for the National Academy of Sciences.

The Carr Medal is given by the Florida State Museum every three to five years in honor of late UF zoology professor Archie F. Carr. Carr was the world's foremost authority on sea turtles. It is in Carr's spirit of dedication and excellence in the biological sciences that the medal is awarded.

SIDA 12(2):429. 1987.

SIDA 12(2):430. 1987.

A FINAL TRIBUTE TO DELZIE DEMAREE

Delzie Demaree, a renowned field botanist, passed away on July 2, 1987 at the age of 97. His endeavours as a naturalist, plant collector, and taxonomist were foremost in his life, and were amply evident in the tributes accorded to him in Sida 9:269-286. 1982.

Delzie was helpful, self-reliant, and resourceful. Although he never intruded into the personal lives of others, Delzie freely expressed idiosyncratic views on all sorts of issues. This befitted him with the self-ascribed label of "Old Scratch."

As a companion on field ventures, Delzie was a joy to those who accompanied him. The warmth of his personality and the zeal he devoted to his work offered an outstanding example to all who knew him. As his nephew I am highly privileged to have known him.—*Robert G. Demaree, Professor Emeritus of Psychology, Texas Christian University, Fort Worth, TX 76129, U.S.A.*

MARY JO LAUGHLIN

(June 5, 1932 - November 14, 1986)

LORI FAIRCHILD and HAROLD E. LAUGHLIN

Heard Museum, Route 6, Box 22
McKinney, TX 75069, U.S.A.

Mary Jo Laughlin was an artist who specialized in floral portraits, of both wild flowers and garden flowers. She was well known throughout Texas and elsewhere for her watercolor paintings, prints and stationery, and for illustrating the book "ABCs of Texas Wildflowers" by Glenna Grimmer.

She was born in Tulsa, Oklahoma, the first of four daughters of Howard F. and Josephine Herlig Hyatt. The Hyatt daughters and their mother were all active in Girl Scouting, which provided their first exposure to and interest in wildflowers and all of nature, an interest which later would guide Mary Jo to a successful artistic career.

As a young girl, Mary Jo pursued this interest by enrolling in a high school summer course in field biology, in which identification of wildflowers was emphasized and the groundwork was laid for botanical accuracy in her paintings years later.

SIDA 12(2):431. 1987.

That summer course introduced Mary Jo to more than wildflower identification: she also was introduced to the student assistant in the class, Harold Laughlin. The two found they shared many common interests, from nature, music and art... to each other. They were married in 1952.

Mary Jo entered the University of Tulsa as an art major and flew through the basic drawing and fundamentals courses. As she progressed, however, Mary Jo grew disappointed: her professors seemed more interested in abstraction and surrealism than in the representational realism that had become her form of artistic expression. Her disillusionment led to a switch in majors, and she received a bachelor's degree in sociology, which she never actively used.

While Harold was in graduate school at the University of Texas, the Laughlins lived for a while in the Texas hill country at Austin and spent two years on the Welder Wildlife Refuge near the Gulf Coast. Each of these environments offered a new and different flora for Mary Jo to study and explore.

Harold later accepted a position at Southeastern State College and the couple moved once again, this time to Durant, Oklahoma. Also new on the faculty were Drs. John and Connie Taylor, both botanists whom Mary Jo utilized as resources for wildflower information. Her level of interest in the subject was raised from "casual" to "serious."

The Laughlins made their last move in 1966, settling down in McKinney, Texas, where Harold assumed the position of the first administrative director of the Heard Natural Science Museum and Wildlife Sanctuary. Their new home provided the perfect setting for Mary Jo's renewed interest in both art and wildflowers. She enrolled in private art lessons and joined the McKinney Art Club.

Mary Jo's first paintings depicted landscapes, old barns and other related subjects, but one day she painted some lovely irises from her garden. She entered her second iris painting in the Art Club's annual Collin County Art Show, and was awarded her first blue ribbon.

Encouraged by this success and inspired by the beautiful wildflowers surrounding her on the Heard Sanctuary, Mary Jo began painting flowers of all kinds. Each new wildflower that bloomed through the seasons presented a new subject and a new challange.

Among garden flowers, the iris held the greatest attraction for her, and soon became her specialty. She loved its many varieties and eventually reached the point where she could draw and paint irises from memory.

SIDA 12(2):432. 1987.

SIDA 12(2):433. 1987.

Mary Jo's botanically accurate style was influenced both by "Roadside Flowers of Texas," written by Howard Irwin and illustrated by Mary Motz Wills, and by the antique botanical prints in the Heard Museum collection, especially those of P. J. Redouté.

A highly skilled illustrator, Mary Jo possessed the ability to sketch with her eyes on the subject more than on the paper, and the confidence to sketch with a watercolor pen rather than a pencil.

She described her style as "bold and masculine," despite the seemingly fragile nature of her subjects. Mary Jo's goal was to create paintings which were both decorative and educational.

She worked quickly, unhampered by her obsession with accuracy, and soon a large volume of paintings began to accumulate. Her works were featured in many solo and group exhibitions in museums, banks, libraries and hospitals, including 26 shows in six states.

Mary Jo was an active member of local art organizations and entered many of their competitions. Although she won a few awards, her talent was often overlooked by judges whose preferences ran toward impressionism rather than her bold realism.

Her extensive reading and studying transformed Mary Jo into a knowledgeable amateur botanist with a concern for the preservation and perpetuation of wildflowers.

In November of 1985 Mary Jo was diagnosed as having cancer. Although illness, chemotherapy and two operations slowed her pace, she continued to paint, completing 41 paintings in the year before her death. One of these, a large composition entitled "Texas Past and Present," won an award in the special Texas Sesquicentennnial division of the 1986 Collin County Art Show, the same show which had launched her flower painting career some 16 years earlier.

Mary Jo published a number of prints of her paintings, and several of her designs can be found on notepapers and stationery. She also prepared bluebonnet designs to be silk-screened on scarves and used for ceramic decals. Each of these products is widely distributed throughout Texas and other states. Another of her bluebonnet designs is used by the Native Plant Society of Texas for brochures and stationery, and yet another is used by Texas Woman's University as a logo on printed materials for the school's annual Wildflower Day, where Mary Jo was honored in 1983 with an award for her wildflower art.

Today Mary Jo Laughlin's works are widely recognized. She leaves a legacy of more than 1,500 flower paintings as well as fond memories of her dedication to art and nature.

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(Continued from front cover)

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